RODENTS FROM THE DESEADAN OLIGOCENE OF BOLIVIA AND THE RELATIONSHIPS OF THE CAVIOMORPHA

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ABSTRACT. The extensive Princeton collections of fossil caviomorph rodents from the early Oligocene Deseadan of Bolivia are described. Much new information is reported concerning the teeth and skulls of *Sallamys pascuali*, *Incamys bolivianus*, and *Branisamys luribayensis*, only one species of each genus being recognized. These are referred to the Echimyidae, Dasyproctidae, and Dinomyidae, respectively. An octodontid, *Migraveramus beatus*, n. gen., n. sp., is described. Lavocat's description of *Cephalomys bolivianus* is briefly reviewed. Two undescribed dasyproctid genera are reported. *Luribayomys masticator* and *Palmiramys waltheri* (the latter from Uruguay) are considered to be *nomina vana*.

The two theories for the origin of the caviomorphs are reviewed. The first states that they are descended from African thryonomyoids that crossed the South Atlantic as waif migrants. The second derives them from Middle American franimorph ancestors that reached South America, also as waif migrants, either directly or through the Antilles.

Eocene hystricognathous rodents have so far been reported only from North America. There is good negative evidence that none reached Europe, but they presumably did reach Asia when that continent was connected with North America, both early and late in the Eocene.

The early Oligocene South American and Egyptian rodent faunas are compared and contrasted, and compared with localized collections of Recent rodents from northeastern Brazil. The differences between and general composition of the various Deseadan local faunas are comparable to those between individual Recent sites. The African Oligocene rodents seem not so diversified as are the modern Australian Pseudomyinae. These latter have achieved their current diversity in about 4.5 m.y. It is proposed that rodents reached Africa no more than this length of time before the lowest fossil levels of the Fayum. The Deseadan rodents are as diversified as are those of the early Miocene of East Africa, and had presumably been in South America about as long before the Deseadan as the thryonomyoids had been in Africa before the early Miocene. This would place the arrival of rodents in South America in the middle Eocene.

The Eocene geography of southern Central America and the Antilles was such that migration of ancestral caviomorphs from Middle to South America, either directly or through the Antilles, would have been entirely possible. It is probable that there was a single invading stock, although there is evidence supporting a distinct origin for the Erethizontidae.

Parasitic nematodes have been cited as supporting a thryonomyoid ancestry of the Caviomorpha. The evidence is reviewed, and it is concluded that there is no valid evidence to support such a hypothesis. In every case of supposed close relationship of nematodes parasitic on Old and New World forms, there is reason to question the validity of the conclusions.

The morphologic evidence used by Lavocat to support the derivation of the Oligocene South American Caviomorpha from the contemporaneous Thryonomyoidea of Africa is reviewed. It is concluded that, although there are many similarities between the Old and New World forms, the evidence indicates that the African forms could (morphologically) have been derived from the South American ones, but that the reverse is structurally impossible. It is concluded that both groups were derived, independently, from Holarctic Eocene members of the Infraorder Franimorpha. The lice and fleas of hystricognaths support the concept that the Hystricognathi are a natural group, but do not allow one to choose between the two hypotheses for the origin of the caviomorphs.

The suprafamilial classification of all hystricognath rodents (Suborder Hystricognathi) is reviewed. Among the Caviomorpha, we now follow a growing consensus that the Families Dasyproctidae, Dinomyidae and Cuniculidae should be transferred from the Superfamily Chinchilloidea to the Superfamily Cavioidea. These families form a group (Series B) distinct from the Families Eocardiidae, Caviidae and Hydrochoeridae (Series A). The Echimyidae are an even more complex group than previously believed, the genus *Chaetomys* (Subfamily Chaetomyinae) being transferred from the Erethizontidae to the Echimyidae. The two subfamilies Capromyinae and Plagiodontinae, formerly included by us in the Family Capromyidae, are likewise here transferred to the Echimyidae. This combines all caviomorphs that ever retain dm_4^4 throughout life in the Family Echimyidae.

The Superfamily Erethizontoidea is retained in the Caviomorpha, in spite of evidence that it is quite distinct from the rest of the infraorder. It was presumably an early offshoot of the basal stock of the Caviomorpha.

The Family Neoepiblemidae is added to the Chinchilloidea as a second family. The Family Heptaxodontidae is left *incertae sedis* as to superfamily.

The Eocene to Oligocene Infraorder Franimorpha, including the Families Reithroparamyidae (new rank), Protoptychidae, Cylindrodontidae, and two genera *incertae sedis* as to family, is considered to have been ancestral to all other hystricognaths. In the Old World, Eocene franimorphs are still unknown, the Chapattimyidae of Pakistan and India being shown to be ctenodactyloids.

The Tsaganomyidae (new rank) of north Asia are considered to be cylindrodont descendants, as are also the Bathyergidae. The two families differ from the cylindrodonts in being fully hystricognathous, and are united in the Superfamily Bathyergoidea. They are both fundamentally protrogomorphous.

No evidence is found for or against deriving the Thryonomyoidea from the Hystricidae. If the two are united at the infraordinal level, the infraorder should be called Hystricomorpha rather than Phiomorpha because of the long priority and general recognition of that term.

Three families of Thryonomyoidea are recognized: Thryonomyidae, Petromuridae and Myophiomyidae. Stromer's genus *Neosciuromys*, placed in synonymy by Lavocat, is re-established.

INTRODUCTION

The Tertiary vertebrates of Bolivia are poorly known. Simpson (1940), in his summary of reported extra-Argentinian Tertiary mammals of South America, could cite only three Bolivian records, all of uncertain age: a tooth referred, perhaps incorrectly, to *Nesodon*; parts of an armadillo, the type of *Dasyptodon atavus* Castellanos; and a jaw fragment of a haplodontheriine toxodontid, the type of *Pachynodon validus* Burmeister. Discoveries of Deseadan faunas in the Cordillera Oriental of Bolivia, not far from La Paz, are therefore of the greatest interest.

The first find was made in the Salla-Luribay Basin, Provincia Loaza, Departamento La Paz, by G. Bejarano in 1962. Dr. L. Braniša began field work there in 1964. With encouragement from the late Professor Glenn L. Jepsen, he undertook intensive work in this and other localities of younger ages for Princeton University. Field, preparational, and other expenses connected with the acquisition by Princeton of the materials brought together by Braniša during 1964–1966 were met by a generous bequest from the late Gordon Barbour, a long-time friend and benefactor of the University, for the express purpose of furthering vertebrate paleontological work in Bolivia. As a result, Princeton possesses an excellent collection of Deseadan mammals from Salla-Luribay. The discovery was announced by Baird *et al.* (1966). From 1965 to 1972 Hoffstetter visited this area and made collections (Hoffstetter, 1968, 1976), and Hartenberger and Villarroel have worked at the locality since then. More recently there have been other expeditions in the area.

At Salla-Luribay, which is some 90 km SE of La Paz, about 450 m of Tertiary continental sediments rest unconformably upon folded Devonian rocks. The lower part of the Tertiary sequence consists of chocolate colored sandstone and conglomerate beds; the upper of well stratified, red and reddish-brown clays and silts with four calcareous beds distributed through the sequence (Hoffstetter, 1976: 4, 6). The lower portion was named the Luribay Conglomerate (Ahlfeld and Braniša, 1960: 132) and the higher the Estratos de Salla, or Salla Beds (Evernden *et al.*, 1966). The vertebrate remains occur in the lower part of the Estratos de Salla, the upper part of that unit and the underlying Luribay Conglomerate apparently being unfossiliferous (Hoffstetter, 1968; a notoungulate skull possibly from the conglomerate has been mentioned by Hoffstetter, 1976: 8). The thickness of the fossil bearing portion of the Salla has not been reported, although Hoffstetter (1976: 8) stated that the fossils are found "depuis la base jusqu'au 3ème niveau calcaire . . . ." We tried to measure the thickness of the fossiliferous zone from the geologic section given by Hoffstetter (1976: Fig. 3), but it would appear that the section is not to scale since, in the figure, the 300 m thick Salla Beds measure 9.5 cm, and the 150 m thick Luribay Conglomerates measure 6 cm. Hoffstetter did not state whether the section represents the maximum thickness of the formation. If it does not, and if the Salla and the underlying Luribay Conglomerate are to scale in the figure, the fossiliferous portion would be about 150 m thick. Ahlfeld and Braniša (1960: 137) note a resemblance between this sequence and the Tertiary Chacarilla Formation of the Altiplano.

Subsequent to the Salla-Luribay discovery, a second, much less extensive and less fossiliferous locality was found at Lacayani, 50 km NW of Luribay and 30 km SE of La Paz (Hoffstetter *et al.*, 1971). The Tertiary deposits there are unconformable upon folded late Cretaceous and Devonian rocks, and are "some tens of meters" in thickness. The lower portion consists of alternating clays, sandstones and yellowish brown conglomerates. This is separated by a 50 cm thick cinerite from the upper, reddish clays, which contain the mammalian remains.

Rodents occur at both localities. Hoffstetter and Lavocat (1970) very briefly described three new genera from Salla: *Sallamys, Incamys*, and *Branisamys*. From Lacayani, Hoffstetter *et al.* (1971) have listed *Scotamys,* a genus known from Patagonia, and an eocardiid. Hartenberger (1975), listing these, has also mentioned "Octodontoidea nov. gen. 1 and 2" from Salla, and described *Villarroelomys*, also from this locality, which we believe (p. 444) to be referable to *Branisamys*. He has further recorded, again from Salla, a species of *Cephalomys*, another genus known from Patagonia. Lavocat (1976) described *Sallamys*, *Branisamys* and *Incamys* in detail, concluded that the type of *Villarroelomys* probably was dm_4 of *Branisamys* (a conclusion that we had already reached), described a second species of *Incamys*, a new species of *Cephalomys* (*C. bolivianus*) and *Luribayomys*, a new genus that he left *incertae sedis*. He was vague (1976: 59) as to whether Hartenberger's *Cephalomys* was or was not the same as *C. bolivianus*. The Princeton collection contains the jaw of a new octodontid genus, additional material of *Sallamys*, extensive and excellent material of *Incamys*, and better material of *Branisamys* than was available to Hoffstetter and Lavocat (1970) or to Lavocat (1976). These specimens are described in detail below.

There can be no doubt as to the Provincial (or Land Mammal) Age of these Bolivian faunas; each contains mammalian species inseparable from Patagonian Deseadan ones or assignable to Patagonian Deseadan genera. The two differ from each other and from Patagonian local faunas—as these latter do among themselves—regarding presence, absence or differing abundances of various faunal elements. It is not at all surprising to encounter such differences between the Bolivian and the Patagonian faunas, separated as they are by nearly 30° of latitude, but it is rather remarkable that all Deseadan local faunas, whether Bolivian or Patagonian and regardless of degree of geographic proximity, should differ to the extent that they do. The rodents, Table 8 (p. 461), are no exception. Each of the better known local faunas—Cabeza Blanca, La Flecha, Salla—contains one species that is predominant numerically and one or two that are moderately common, whereas the rest are represented only by one or two specimens. In no case is the predominant species the same in more than one locality. The question is: are these differences due primarily to age or primarily to the sampling of different ecologies?

Both views have been advanced. Hartenberger (1975) has tentatively suggested, as a working hypothesis, that Rinconada de los Lopez (Scarritt Pocket) is the earliest local fauna, Salla intermediate, and La Flecha and Cabeza Blanca the latest. This was based on the primitive nature of *Platypittamys*, on the presence of a species in the Salla local fauna (his Octodontoidea nov. gen. 1) that "on dental characters could be considered a descendant of *Platypittamys*," and on the Salla species of *Cephalomys*, stated to be small and more primitive than those occurring at Cabeza Blanca and La Flecha. Wood (1949) had previously considered Rinconada de los Lopez as being earlier than the others, also on the basis of *Platypittamys*. The alternative, ecological hypothesis is based on the local faunas as wholes. In no instance (with the possible exception of Hartenberger's octodont) is it demonstrated that a species in one local fauna is ancestral to a species in another (Wood and Patterson, 1959: 300). As Hoffstetter *et al.* (1971) have put it: ". . . les faunes . . . appartiennent au Déséadien . . . sans qu'on puisse exclure la possibilité de légers décalages chronologiques, de toute façon minimes."

In agreement with these authors, we doubt that anyone would be prepared to assert that all Deseadan local faunas were exactly synchronous. Granting this, were the differences in age between them minimal in the geological sense or sufficiently long to permit evolution to or toward the species level? Support for the latter possibility must, it would seem, come from the rodents since other faunal elements do not, so far as known, favor it. The most suggestive evidence, as yet undocumented, is of course provided by Hartenberger's remark that his Salla Octodontoidea gen. nov. 1 could be descended from *Platypittamys* (a claim he has not made concerning the relationships of the *Cephalomys* present at Salla to those occurring at La Flecha and Cabeza Blanca). It is possible, however, for more primitive and more advanced, yet closely related, species to coexist in the same local fauna. *Deseadomys loomisi*, type and only known specimen from Cabeza Blanca, is larger and more advanced as regards metalophid reduction than *D. arambourgi*, type from La Flecha. If knowledge rested there it could very plausibly be argued that the latter was ancestral to the former, but negating this possibility is a specimen from Cabeza Blanca that can be referred with confidence to *D. arambourgi* (Wood and Patterson, 1959: 305). As a minor item of evidence suggesting a close approximation in time between Cabeza Blanca and Salla, we may point to the presence at the former of an isolated P^4 that we are unable to distinguish from corresponding teeth of *Incamys bolivianus*, the commonest rodent at Salla (see Table 8 and p. 429).

On the age difference side of the argument, it seems probable that the Deseadan rodents, not yet fully beyond the first flush of their initial adaptive radiation but nonetheless the most abundant group of Deseadan fossils, were evolving rapidly (more so than other faunal elements whose ancestors had been in South America for millions of years before the rodents arrived there) and should therefore be the best indicators of temporal differences within that Age. This may indeed be so, but the documentation of it is not yet satisfactory. However, the upper premolars are three-crested in all or nearly all (see below, p. 495) of the Patagonian genera in which they are known, and four- or five-crested in the ones from Salla. We believe the three-crested pattern to be the primitive one. This suggests, to Wood at least, that the Salla deposits may be later than those in Patagonia. We are open minded as regards the two hypotheses, although we must confess to differing preferences: Patterson, in agreement with Hoffstetter (1976: 11–12), inclining toward ecological differences; Wood toward age ones. (The composition of Deseadan rodent faunas is further discussed below, pp. 460–471.)

As concerns the age of the Deseadan as a unit, welcome new evidence is at hand. Marshall *et al.* (1977) have reported that a basalt above Deseadan sediments at Pico Truncado has an age of 33.6 ± .4 m.y.b.p., and another, at Cerro Blanco, apparently directly conformable upon Deseadan sediments, one of 35.4 ± .4 m.y.b.p. These authors report that the basalts record a period of volcanic activity "around 34–35 mybp," and this "is tentatively accepted as an approximate terminal date for known Deseadan." They regard the 33.6 m.y.b.p. date as being a little post-Deseadan. It is gratifying to see the previous consensus as to early Oligocene age confirmed by the new evidence; our suggestion (1959: 388) that the Deseadan was early but not earliest Oligocene may not have been too wide of the mark. How long the Age may have lasted remains uncertain. We utilize the earlier Tertiary epoch boundaries of Berggren and Van Couvering (1974: Fig.

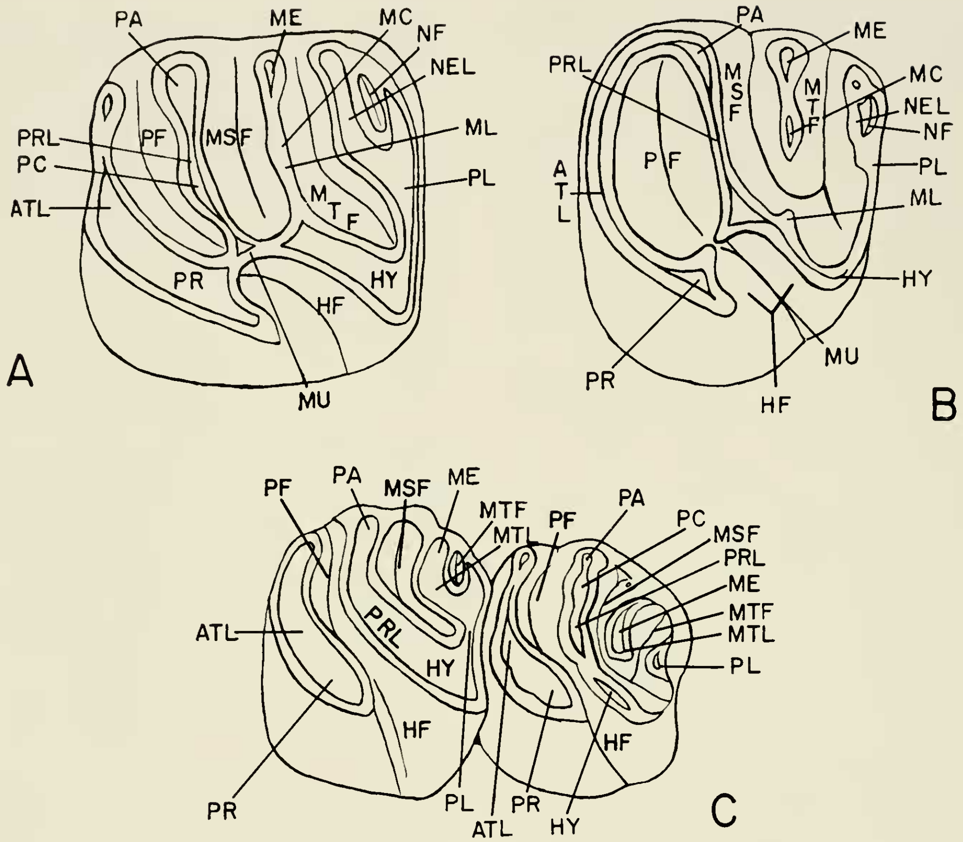

Figure 1. Nomenclature of parts of caviomorph upper cheek teeth. Anterior ends of all teeth to the left. A. *Protosteiromys medianus*, LM¹ or ². B. *Protosteiromys medianus*, LM³. C. *Incamys bolivianus*, LM²⁻³.

Abbreviations: ATL—anteroloph; HF—hypoflexus; HY—hypocone; MC—metaconule; ME—metacone; ML—metaloph; MSF—mesoflexus or mesofossette; MTF—metaflexus or metafossette; MU—mure; NEL—neoloph; NF—neofossette; PA—paracone; PC—protoconule; PF—paraflexus or parafossette; PL—posteroloph; PR—protocone; PRL—protoloph. Flexi are unworn valleys that become fossettes with wear.

1). They date the beginning of the Oligocene at 37.5 m.y.b.p.

Most unfortunately, no radiometric dates are available for the Mustersan. The duration of the hiatus, undoubtedly long, between this Age and the Deseadan can only be guessed at; a reasonable estimate is that it lasted throughout most or all of late Eocene time and perhaps into earliest Oligocene as well. Absence of rodents—and of primates—in Mustersan and earlier deposits is the basis for the view that the earliest members of these orders to reach South America arrived at some time during the Mustersan-Deseadan hiatus. Just when they did so and whether or not they arrived at essentially the same time are questions that will remain unanswered until the hiatus is filled. (One small local fauna of very peculiar facies, the Divisadero Largo, which contains no rodents or primates, is pre-Deseado and post-Musters.) The new Bolivian evidence of course does not directly contribute to determining the time, within the hiatus, when the rodents reached South America.

Hoffstetter and Lavocat (1970) did not

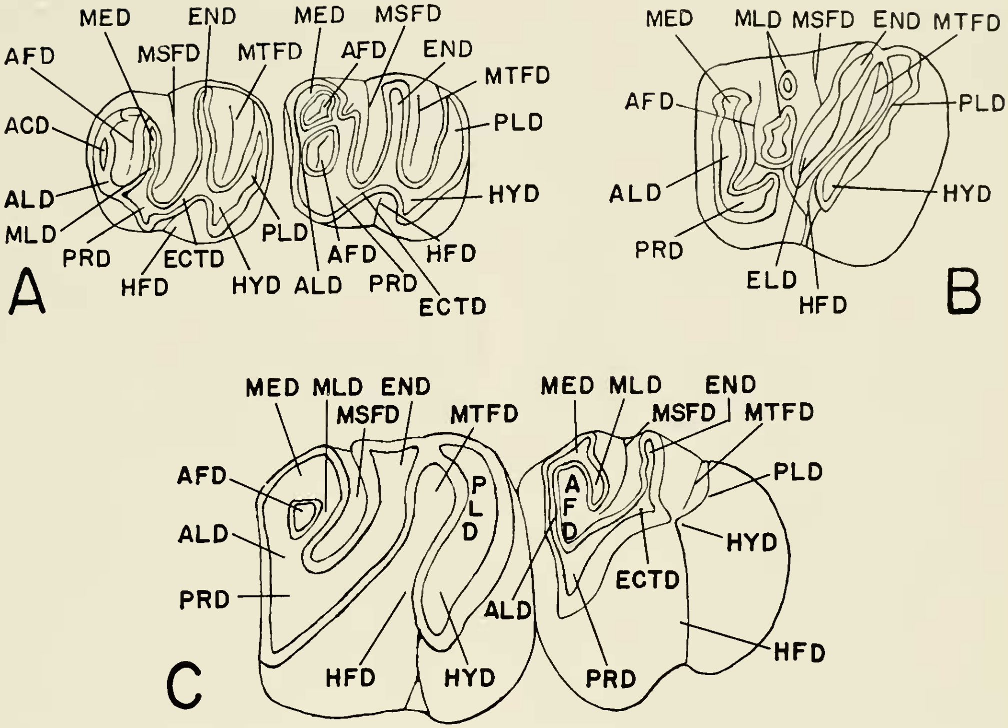

Figure 2. Nomenclature of parts of caviomorph lower cheek teeth. Anterior ends of all teeth to the left. A. *Migraveramus beatus*, RP$_4$–M$_1$, reversed. B. *Incamys bolivianus*, LP$_4$. C. *Incamys bolivianus*, LM$_{2-3}$.

Abbreviations: ACD—anteroconid; AFD—anterofossettid; ALD—anterolophid; ECTD—ectolophid; END—entoconid; HFD—hypoflexid; HYD—hypoconid; MED—metaconid; MLD—metalophid or metalophulid II; MSFD—mesoflexid; MTFD—metaflexid or metafossettid; PLD—posterolophid; PRD—protoconid. Flexids are unworn valleys that become fossettids with wear.

allocate their three new genera from Salla to families. Hartenberger (1975) placed *Sallamys* in the Octodontoidea, *Incamys* in the Chinchilloidea, and *Branisamys*, with a query, in the Dinomyidae. We had independently arrived at broadly similar conclusions (cf. Patterson and Pascual, 1972: 278), and present evidence in the following pages that *Sallamys* was a member of the Echimyidae, *Incamys* of the Dasyproctidae, and *Branisamys* of the Dinomyidae—without query. A new genus, *Migraveramus*, is referred to the Octodontidae. One specimen of Lavocat's hypodigm of *Incamys bolivianus* represents, we believe, an undescribed dasyproctid genus. Salla thus adds a family to the six previously represented in the Deseadan. In 1959 we inadvertently cited seven families on page 389, thus contradicting our correct statement on page 284 (with Lavocat, we are unable to agree that Hartenberger's *Villarroelomys* is referable to the Hydrochoeridae). Lavocat (1976) also placed *Sallamys* in the Echimyidae and *Incamys* in the Dasyproctidae, but erred, we believe, in also including *Branisamys* in that family. Hoffstetter and Lavocat (1970), on the basis of some points of similarity in cheek tooth structure between these forms and the approximately contemporaneous Fayum rodents, favor descent of caviomorphs from (as yet unknown) African Eocene thryonomyoids, which they believe to have been rafted across a then narrower South Atlantic Ocean. This suggestion has been further elaborated upon by Lavocat (1973, 1976). We do not find the evidence presented in support to be any more convincing than we did a few years ago (Wood and Patterson, 1970). This and related topics are treated at some length in the concluding sections.

Cheek tooth terminology is as previously employed by us (1959: 286–288, Fig. 1). The terminology is repeated, and somewhat enlarged, in Figs. 1–2; it differs in important respects from that adopted by Lavocat (1976), stemming from his belief that the more complex Deseadan caviomorph teeth are primitive and that the less complex ones are specialized, whereas we take the opposite point of view.

Measurements of hypsodont rodent teeth (both cheek teeth and incisors) may vary with the age of the animal and with the precise manner in which the measurements have been made. They were made, for this study, as previously described (Wood and Patterson, 1959: 288–289). We have been encouraged, however, by the fact that, while the coefficient of variation for our measurements is often high (Tables 3–4; Wood and Patterson, 1959: Tables 3–5), it is usually less than 10. The measurements that give the highest variation are transverse diameters of upper cheek teeth (Table 3), where the curvilinear eruption of the teeth often produces an elongate buccal shelf; the anteroposterior diameter of M_3, due to variation in the measurement of the long posterior slope because of loss of the alveolar rim behind the tooth; and the actual measurements (as opposed to the ratio) of the incisors, due to diametric enlargement of these teeth with age. The reasons behind the variability of the tooth measurements are discussed in more detail below (p. 416).

We have reviewed the classification of the Suborder Hystricognathi in the final part of our discussion. In this paper, we have made the explicit assumption that hystricognathy arose once in the evolution of the rodents, and that, therefore, all hystricognathous rodents are related, and are more closely related to each other than any are to other groups of rodents. There is some documentary support for this assumption, but it cannot be taken to have been demonstrated. However, if hystricognathy arose independently, several times, as parallelisms, it means that there is no justifiable basis, at the present time, for grouping rodents at the subordinal level, and that no attempts at determining relationships between larger taxonomic groups of rodents should be made until there is full documentation for the evolutionary sequences involved (see below, pp. 476–477).

For example, at the present time, there is no final proof that the various families of caviomorphs have a common South American ancestor. We believe that they did have such a common ancestry, but, since seven families were already present in the Deseadan, when the caviomorphs first appear, the conclusion that they were the descendants of a single invading stock is an unproven assumption on our part.

As we classify them (see below, pp. 522–523), the Old World hystricognaths are divided into three groups that, in our opinion, cannot at present be demonstrated to have had a common ancestry later than the Eocene franimorphs. The Hystricomorpha contain a single family and the Bathyergomorpha contain two families, one Asian and one African. The African Thryonomyoidea perhaps should be referred to the Hystricomorpha and perhaps deserve recognition as a separate infraorder, the Phiomorpha. Lavocat (1973, 1976) united all the Old World hystricognaths in the Infraorder Phiomorpha. To avoid the probability of confusion between our usage and that of Lavocat, we have avoided using the infraordinal terms Phiomorpha, Bathyergomorpha, and Hystricomorpha, and have, instead, used the suprafamilial or familial terms, everywhere except in our final section, Classification of the Suborder Hystricognathi.

The manuscript of this paper had been largely completed at the time of the death of the senior author. All of the first half—Taxonomy and Morphology—was in order; the various sections of the Discussion had been written, although some were not in their final form and, in some instances, no final decision had been reached as to their sequence. Extensive notes by Patterson were also available. In general, it is Wood's belief that the statements in the discussion are the opinions of both authors, unless the contrary is explicitly stated. Some sections that had to be prepared essentially or entirely by Wood are so indicated. Any errors that may have developed in the final preparation of the paper must be assumed to be the sole responsibility of the junior author.

ACKNOWLEDGMENTS

We are deeply indebted to the late Professor Glenn L. Jepsen for permission to study the Salla collection in Princeton University, and to Drs. Vincent J. Maglio and Donald Baird for continuing courtesies in this connection. We have received assistance in a number of matters from: Professor Robert W. Fields, Geology Department, University of Montana, Missoula; Dr. J.-L. Hartenberger, Laboratoire de Paléontologie, Université de Montpellier; Dr. P. E. Vanzolini and Dr. Lindolpho R. Guimarães, Museu de Zoologia da Universidada de São Paulo; and Dr. John H. Wahlert, then of the American Museum of Natural History. Dr. J. J. Raab, DDS, of Cape May Court House, N.J., made the X-ray photograph of the specimen of *Sallamys pascuali* described below (p. 383), and Dr. Luiz Fernando da Castro Leite, C. D., of São Paulo, made those of *Chaetomys* discussed on p. 394. Professor Elwyn L. Simons and Dr. Grant E. Meyer have generously contributed information about the Yale Fayum collections. Dr. Hartenberger has provided us, through the courtesy of Dr. Lavocat, with the numbers of specimens of various taxa of rodents included by the latter in his study of the Salla-Luribay rodents, data not given in the published report (Lavocat, 1976). Hartenberger stated (*in lit.*, 10 July 1976) that his own large collections of Salla rodents were still unidentified. We are grateful to Dr. R. W. Wilson of the Museum of Natural History, The University of Kansas, who has critically reviewed the manuscript and who has made a number of suggestions on points that needed clarification. We have attempted to carry out all of his suggestions.

The senior author had the benefit of numerous discussions with Dr. Ernest E. Williams of the Museum of Comparative Zoology, covering many aspects of the present paper. The major concrete suggestion here incorporated is that mentioned on p. 461, but there were many others of lesser fundamental import.

This study has been aided by awards to Wood of Grants 148 and 150 from the Marsh Fund of the National Academy of Sciences, and to Patterson from the Fundação de Amparo è Pesquisa do Estado de São Paulo. The drawings of Miocene thryonomyoids from Southwest Africa (Fig. 28G–K) were made by Wood during his tenure of a National Science Foundation Senior Post-Doctoral Fellowship in 1967–68. Illustration and publication have been aided by the Gordon Barbour fund of Princeton University. Continuing support has been received by Wood from the Biology Department, Amherst College.

ABBREVIATIONS

Abbreviations used for the names of museums:

ACM—Pratt Museum of Amherst College
AMNH—American Museum of Natural History

AMNH Mam—American Museum of Natural History, Dept. of Mammalogy
FMNH—Field Museum of Natural History
GB—Colección Geobol, La Paz
MACN—Museo Argentino de Ciencias Naturales
MCZ—Museum of Comparative Zoology
Munich—Institut für Paläontologie und historische Geologie, Universität München
MZUSP—Museu de Zoologia da Universidade de São Paulo
PU—Princeton University, Department of Geology
UCMP—University of California (Berkeley), Museum of Paleontology
YPM—Yale Peabody Museum

TAXONOMY AND MORPHOLOGY

Order **RODENTIA** Bowdich 1821
Suborder **HYSTRICOGNATHI** Tullberg 1899
Infraorder CAVIOMORPHA Wood and Patterson 1955 (in Wood, 1955, as a suborder)
Superfamily OCTODONTOIDEA Simpson 1945
Family OCTODONTIDAE Waterhouse 1839

Migraveramus[1] new genus

Diagnosis. Lower cheek teeth low crowned lingually and of medium height buccally, fully crested; dm_4 replaced at normal stage of life; P_4–M_2 fully tetralophate, with crests nearly perpendicular to anteroposterior axis; an anteroposterior crest crossing lingual part of anterofossettid; lower incisor with flat anterior face; coronoid process passing alveolar border at middle of M_3; angular process leaving body of ramus beneath middle of M_2; mental foramen in front of P_4, opening anteriorly and ventrally.

Type Species. Migraveramus beatus.

Distribution. Deseadan Oligocene of Bolivia.

Migraveramus beatus[2] new species
Figure 3

Diagnosis. As for the genus; measurements as given in Table 1.

Type. PU no. 21948, partial right ramus with P_4–M_2 and the base of the incisor, Branisa field no. 6515.

Hypodigm. Type only.

Horizon and Locality. Deseadan early Oligocene, lower part of Estratos de Salla; Salla-Luribay Basin, Bolivia.

Description. The three anterior lower cheek teeth (P_4–M_2; Fig. 3A) are all four-crested. For terminology of parts of teeth, see Fig. 2. The anterofossettid is crossed, on all, by an anteroposterior crestlet of varying prominence, arising from the anterolophid and reaching the lingual tip of the metalophid (Fig. 3A). The metalophid does not unite directly with the metaconid, but with a crest running buccally from it. On M_2, the connection has just been established (Fig. 3A). The lingual part of the anterofossettid basin is very shallow, and would be eliminated with but little wear. The protoconid is set off from the ectolophid by an angulation on P_4. A distinct anteroconid is present on this tooth (Fig. 3A). There is no trace of a mesoconid or mesolophid on any of the teeth. The hypolophid is connected with the hypoconid by a narrow isthmus arising from the front of the latter. It is marked by a swelling midway between the ectolophid and entoconid. The posterolophid shows indications of there having been a hypoconulid. The anterofossettid is closed lingually; the mesoflexid and metaflexid are open on all three teeth, the mesoflexid being the deeper; the hypoflexid is the deepest of all. The buccal cusps are somewhat higher than the lingual ones; there is little difference in height between the an-

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[1] The pluperfect of *migrare*, to migrate, plus *mus*, a rodent, in indication of our belief that this genus is closely related to the caviomorphs that first migrated to South America.

[2] Named for the Little Angel.

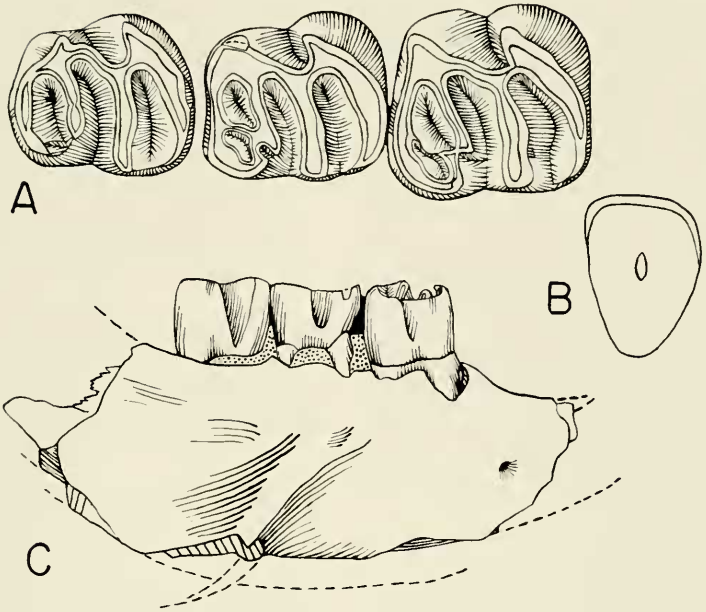

Figure 3. Teeth and jaw of *Migraveramus beatus*, gen. et sp. nov., PU no. 21948, type. A. RP_4–M_2, ×10. B. Cross section of RI_1, beneath diastema, ×10. C. Lateral view of right lower jaw, ×5.

terior and posterior cusps of each side. The base of the enamel is nearly horizontal around the teeth. The anterior root of dm_4 is still present in front of P_4 (Fig. 3C).

The incisor has a flat anterior face, with the enamel extending fairly far around on both sides (Fig. 3B). The pulp cavity, below the diastema, is small and oval.

The mandible is badly damaged. No features of any significance were observed on the medial side. The mental foramen (Fig. 3C) is about half way up the side of the mandible, a short distance in front of the anterior root of P_4, and faces forward and downward. The anterior tip of the masseteric crest lies on the upper third of the mandible, beneath the rear of P_4, whence it curves posteroventrad and increases rapidly in prominence. Only the beginning of the coronoid process is visible, but it passed the alveolar border near the front of M_3 (Fig. 3C).

Relationships. The mandible agrees with that of the Deseadan octodontid *Platypittamys* (Wood and Patterson, 1959: 298) in the absence of any distinct scar for the *M. masseter medialis, pars anterior*, suggesting that this muscle was poorly developed.

The pattern of the lower molars agrees with that of *Platypittamys* alone among Deseadan rodents—there are four transverse crests, the two anterior and the two posterior being widely separated by the deep mesoflexid (Wood, 1949: Fig. 3C,D). As in *Platypittamys* (Wood, 1949: Fig. 3C; M_2), the metaconid is somewhat isolated from the metalophid. The

TABLE 1. MEASUREMENTS, IN MM, OF TEETH OF *Migraveramus beatus*, TYPE, PU NO. 21948, RIGHT.

P_4 anteroposterior	2.38	M_2 anteroposterior	2.48
width, metalophid	1.74	width, metalophid	2.53
width, hypolophid	2.14	width, hypolophid	2.49
M_1 anteroposterior	2.40	I_1 anteroposterior	2.16
width, metalophid	2.02	transverse	1.50
width, hypolophid	2.26	ratio	.70

anteroposterior bar across the anterofossettid also appears in *Platypittamys* (Wood, 1949: Fig. 3D). The pattern of P_4 of the two genera, however, is quite distinct, that of *Migraveramus* being fully molariform, whereas P_4 of *Platypittamys* has no trace of a posterolophid, and the anterior half is not so molariform as in *Migraveramus*.

The cheek teeth of *Migraveramus* are appreciably higher crowned than those of *Platypittamys*.

The incisor (Table 1) is considerably wider than that of *Platypittamys* (width/length ratio = .70 as opposed to .39 and .57 in the two specimens of *Platypittamys* given by Wood, 1949: Table 2). The general shape of the incisors, is, however, identical.

Wood and Patterson (1959: 295) agreed with Wood (1949: 45) that *Platypittamys* and its relatives (the primitive octodontids, of which *Platypittamys* was then the only Deseadan representative) were "ancestral, at least structurally, to all rodents . . . included in the Caviomorpha, with the possible exception of the Erethizontidae." We still take this position, and feel certain, among other things, that the teeth of *Migraveramus* are completely different from those of any thryonomyoid and demonstrate the origin of the Caviomorpha from a tetralophate ancestry, of the type found during the middle and late Eocene in North American rodents, including franimorphs as well as paramyids and sciuravids. The same pattern is found in the latest Eocene and Oligocene ischyromyids.

The significance of the peculiar pattern of P_4^4 of *Platypittamys* is still uncertain. Incidentally, it should be mentioned that the "recently discovered but still undescribed lower Gray Bull paramyid" cited by Wood and Patterson (1959: 296) in this connection, is *Franimys amherstensis* from the latest Paleocene Clark Fork beds, the earliest known hystricognath rodent. The fully molariform premolar of *Migraveramus* suggests that the ancestral stock of the caviomorphs may have had tetralophate premolars as well as molars, agreeing in this with the Eocene and Oligocene North American forms mentioned above. This is supported by the fact that, in a completely unrelated group of rodents, a somewhat analogous pattern of P_4 occurs, clearly as the result of secondary reduction of complexity (*Meliakrouniomys*, Wood, 1974a: 79–80, Fig. 33C).

We conclude that the octodontids are the most primitive of the Deseadan rodents, and that the nearest known approach to the ancestral condition is represented by *Migraveramus*.

Family ECHIMYIDAE Gray 1825

We believe that this family should be dated from Echimyna Gray 1825, the first usage covering the modern family in essential concept though not in spelling, rather than from Waterhouse 1839.

Subfamily HETEROPSOMYINAE Anthony 1917

Sallamys Hoffstetter and Lavocat 1970

Emended Diagnosis. Infraorbital foramen and area of origin of *M. masseter medialis, pars anterior* large (Hoffstetter and Lavocat); cheek teeth brachydont, uppers higher lingually than labially, lowers higher labially, both about as in Paramyidae and Reithroparamyidae; dm_4^4 replaced; dm^3 possibly present; P^4 variable, trilophate or incipiently tetralophate, with or without mure, paracone and buccal tip of anterocone distinct in early stages of wear; M^{1-3} notably wider than long, tetralophate with lophs directed transversely, metafossette shallow; P_4 with fully formed hypolophid, small metalophid spur, metaconid distinct in early stages of wear; M_{1-3} basically trilophate with minute vestiges of metalophid; anterolophid, hypolophid and lingual portion of posterolophid transverse; dm_4 replaced in normal manner, very complex, with two labial, one anterolabial, two lingual flexids.

Type Species. Sallamys pascuali Hoffstetter and Lavocat 1970.

Distribution. Deseadan Oligocene of Bolivia.

Sallamys pascuali Hoffstetter and Lavocat 1970
Figures 4–5

Diagnosis. As for the genus. Tooth measurements as given in Table 2.

Type. Anterior part of skull, preserved back to the glenoid on the left side, with articulated jaw and including a complete set of cheek teeth, in "ma collection personelle, déposée à l'Institut de Paléontologie du Muséum Nationale d'Histoire Naturelle, à Paris" (Hoffstetter, 1976: 13); listed without museum number by Hoffstetter and Lavocat (1970: 174) and without museum reference as "SAL 101A (Crâne) et SAL 101B (Mandibule)" by Lavocat (1976: 23).

Referred Material. Eleven specimens in the Princeton collections, listed in Appendix 1 (p. 528).

Horizon and Localities. Deseadan, early Oligocene, lower part of Estratos de Salla, Salla-Luribay Basin, Bolivia. PU nos. 20906–20911 were found at Pampa Tapial in a grayish-white, gypsiferous clay some 10 m above a 30–50 cm thick bed of greenish-gray limestone, within an area 20 by 20 m; PU nos. 20912–20913 are from dark red to reddish-brown rocks in the lower part of the Salla succession; and PU nos. 20982 and 21727 are from Tomolo (so spelled by Braniša) midway between Salla and Aroma (L. Braniša, field notes). We doubt whether Tomolo is the same as the locality identified by Hoffstetter as Toloma (1976: Fig. 2), since Hoffstetter stated (1976: 14) that he found no rodents at Toloma.

Description. Beyond stating that the infraorbital foramen was large and that the area of origin of *M. masseter medialis, pars anterior* was extensive, Hoffstetter and Lavocat (1970: 173) gave no account of cranial structure. The skull was, however, described in detail by Lavocat (1976: 24–26).

The material at our disposal of course reveals very little of the skull structure. The maxillary fragment shows no trace of an alveolus for P^3. There is, however, a slight elevation on the curved surface of the maxilla anterad and slightly mesiad of the anterobuccal root of P^4 (Fig. 4A; X). When viewed with the light shining from the correct angle, this area is seen to have quite a different luster from that of the adjacent areas of bone, and to be bifid posteriorly. This area may represent the closed alveolus of a shed dm^3, a tooth now known to occur in some Deseadan caviomorphs. An X-ray photograph shows that this area is clearly differentiated from the adjacent bone, but that there is no identifiable tooth structure.

The zygoma arises from the maxilla anterior to P^4 as in echimyids generally, and the ventral surface of the maxilla ascends abruptly anterior to P^4. Medial to this tooth is a concavity (Fig. 4A; IF), which is the posterior end of a very elongate incisive foramen that reaches back to the middle of P^4, farther than Lavocat (1976: 26) was able to trace the foramen, since this area is still buried in matrix in the type (Lavocat, 1976: Pl. 1, Fig. 3). The foramen extends farther posterad than in any of the Santa Cruz rodents figured by Scott (1905), or than in any of the other known Deseadan caviomorphs except *Incamys* (Fig. 14A). There are similarities to that of *Metaphiomys*, although it is not sunk in a palatal depression, as is the case in the Fayum form (Wood, 1968: Fig. 6A). The dorsal view of the maxillary fragment shows the passage of the sphenopalatine foramen (Fig. 4B; SPF), running anteromesially from the orbit to the nasal passage. The lateral wall of the nasal passage, anterior to the sphenopalatine foramen, contains a groove that runs as far forward as the bone is preserved (Fig. 4B; NLC?). This is believed to be

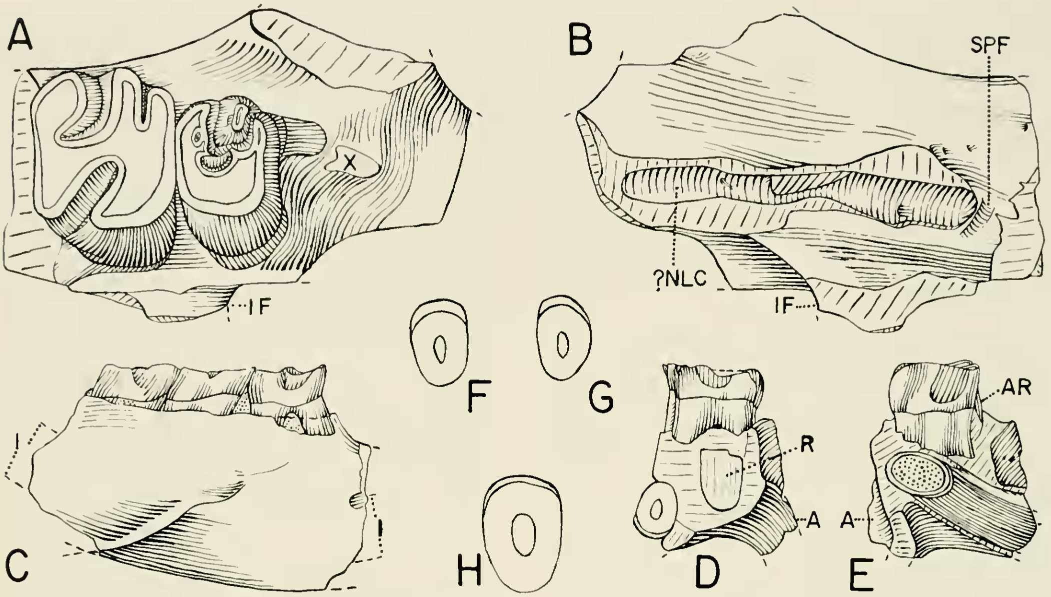

Figure 4. Teeth and bones of *Sallamys pascuali*. C–E. ×5; others, ×10. Dotted areas are matrix. A–B. Maxillary fragment containing RP^4–M^1, PU no. 20906. A. Occlusal view, anterior end to the right. B. Dorsal view, anterior end to the left. C. Lateral view of lower jaw, PU no. 20907, with anterior part of diastema, mental foramen, angular process and incisor added from PU no. 20911. D–E. Anterior and posterior ends of PU no. 20912. D—anterior view, broken through posterior root of P_4; E—posterior view, broken just behind M_2; F–H. Cross sections of lower incisors, seen from the front. F. PU no. 20913, LI_1, below diastema. G. PU no. 20909, RI_1, below front of dm_4. H. PU no. 20912, LI_1, below front of M_1.

Abbreviations: A—angular process; AR—anterolingual root of M_2; I—projection of position of incisor; IF—posterior end of incisive foramen; NLC?—?nasolacrimal canal; R—posterior root of P_4; SPF—sphenopalatine foramen; X—possible unerupted dm^3 within the bone.

the nasolacrimal canal, which apparently descended vertically from the lacrimal foramen, above M^1, and then turned abruptly forward. This groove is separated from the sphenopalatine foramen by a wall of bone in PU no. 20906 (Fig. 4A). If this is the nasolacrimal canal, its course was quite different from that in *Incamys*, in which it seems to have followed a straight line from the lacrimal foramen to the nasal passage. In *Branisamys*, the canal curved more ventrally than in the other genera, and extended forward as a distinct passage (Figs. 24A, 25B). Three small nutritive foramina are present in the floor of the orbit, just anterior to the sphenopalatine foramen. There is a shallow groove on the floor of the infraorbital foramen, presumably marking the course of the infraorbital nerve and blood vessels.

The masseteric crest of the mandible arises high on the horizontal ramus beneath the posterior part of P_4 (Fig. 4C), and becomes very large as it runs downward and backward. Anteriorly, the incisor lies mesiad of the roots of the cheek teeth (Fig. 4D); but, farther back, the incisor curves laterad and crowds the posterior root of M_2 (Fig. 4E) and all the roots of M_3. This is accompanied by a spiral twisting of the incisor (Fig. 4D–E). The exact location of the mental foramen caused us some uncertainty. In PU no. 20907, the break at the anterior end of the bone passes through what looks like a small mental foramen very high on the bone. However, in PU nos. 20908, 20911 and 20913, there clearly is a fair-sized foramen, just in front of P_4, slightly above the middle of the lateral side of the mandible, and at the level of the upper edge of the incisor. There are several nutrient foramina on the medial surface of the jaw below the molars and above the incisor. In the contemporary *Xylechimys* and *Deseadomys arambourgi* (but not in *D. loomisi*) the masseteric crest begins beneath M_1, and in *D. arambourgi* there are two mental foramina, the posterior beneath the middle of P_4 (no such foramen is present in any of our specimens of *Sallamys pascuali*) and the anterior beneath the middle of the diastema, somewhat farther forward than in *D. arambourgi* (Wood and Patterson, 1959: Fig. 6).

The cheek teeth, notably the uppers, increase in width posteriorly, to M_2^2. For terminology of the parts of the cheek teeth, see Figs. 1–2 (pp. 376–377). According to the illustrations given by Hoffstetter and Lavocat (1970) and by Lavocat (1976: Pl. 1, Fig. 5), M_3^3 are slightly smaller than M_1^1 (Lavocat, 1976, unfortunately gave no measurements except the length of the tooth row for any of the Salla rodents, stating, on page 22, that he had not included other measurements because Hartenberger was working on a statistical study). The teeth are brachydont, although the uppers show some unilateral hypsodonty, the height of crown on the lingual side being about twice that on the labial (Fig. 5B). The base of the enamel is essentially horizontal around the tooth. As indicated below, in our opinion the teeth are clearly four-crested (Fig. 5A). Lavocat (1976: 29–30) describes these teeth as four-crested, but believed that he could find the remnants of a fifth, the mesoloph (see below, p. 386). On a subsequent page, however, he concluded that *Sallamys* showed "clairement un morphologie pentalophodonte" (1976: 43), which seems to us to be stretching a point.

In the lower teeth, the crown is highest at the hypoconid, but the disparity in height of various parts of the crown is less pronounced than in the uppers. The molars are wider relative to length than in *Deseadomys*, resembling those of *Platypittamys* in this respect and also in the very transversely directed lophs and lophids. Except as noted below, our descriptions of the teeth are based on the Princeton specimens.

The contour of P^4 is oval, and the tooth is notably smaller than M^1 (Fig. 4A). Anteroloph, protocone and posteroloph sweep around the anterior, lingual and posterior faces of the tooth, and a slight vertical depression on the lingual face (too faint to show on Fig. 4A except as an irregularity of the enamel-dentine border) may perhaps mark an exceedingly incipient separation of a hypoflexal division. Lavocat (1976: 29) did not see such a depression, and none shows on his stereophoto (*op. cit.*: Pl. 1, Fig. 5). The labial extremity of the anteroloph closely approaches the paracone, from which it is separated by a shallow notch; with a little more wear the two would have united. The paracone is large, elongate transversely and independent, the protoloph being incomplete. As a result of this, the paraflexus and the mesoflexus are confluent, forming a deep U-shaped fossa in the center of the tooth. This is partially divided by a thin, low ridge—the serial homolog of the mure of the molars—connecting a spur from the protocone to one from the posterior crest and isolating a deep central basin. This ridge is absent on the type (Lavocat, 1976: Pl. 1, Fig. 5). The posterior crest is rather wide in its labial half, where it contains a small fossette, the serial homolog of the molar metafossette. The tooth is thus incipiently tetralophate and, for an echimyid, is advanced for its time in this feature. Hoffstetter and Lavocat state that, in the type, there is a "vestige" (rudiment, in our opinion) of the metaloph on the anterior face of the posteroloph, but this is not shown in their figure. Their figure does, however, show a small crest on the posterior side of the protoloph (1970: Fig.), which we believe to be homologous to what we interpret as the mure (Fig. 4A). However, Lavocat (1976: 20) does not mention either structure, and his stereophoto (*op. cit.*: Pl. 1, Fig. 5) shows neither one.

In this respect, P^4 of PU no. 20906 is at once more and less advanced than in contemporary octodontoids. It is more advanced than that of the type (Hoffstetter and Lavocat, 1970: 173, Fig.) in the complete incorporation of the anterocone in the anteroloph, the presence of the mure, the fossette in the posteroloph, and the incipient lingual division. It is less advanced than those of *Platypittamys* and *Deseadomys arambourgi* in the isolation of the paracone; more advanced than either in the incipient division of the posteroloph; and more advanced than *Platypittamys* in the possession of a mure. What all this indicates, we suspect, is merely that octodontoids, and indeed all caviomorphs, were actively undergoing molarization of the premolars during Deseadan time and that the process was accompanied by much individual and populational variation. This definitely indicates, to us, that the ancestral caviomorph stock did not have fully molarized upper premolars.

The first upper molar of PU no. 20906 (Fig. 4A) is worn in a manner slightly different from that of the corresponding tooth of the type. The metafossette has been worn away, and the paraflexus has been reduced to a very shallow groove, although it is deeper than in the type (Lavocat, 1976: Pl. 1, Fig. 5). The hypoflexus is still much more widely open than is shown by Hoffstetter and Lavocat (1970: Fig.) or by Lavocat (1976: Pl. 1, Fig. 5). The deep mesoflexus turns posteriorly at its lingual extremity, revealing that, as in M^1 of the type, the metaloph had shifted its moorings from the mure to the posteroloph. In the type, but not in the Princeton specimen, the former site of metaloph attachment is marked by a minute projection on the mure. Lavocat (1976: 30) discussed this projection as "un portion linguale rudimentaire du mésolophe," an interpretation that seems to us to be without justification. The crestlet is aligned with and points toward the metacone, which should not be true of a mesoloph. It lies well behind the middle of the mure, whereas a mesoloph normally lies at the center of the mure. Lavocat pointed out that there is a low ridge, below the wear surface of M^1 of the type, that connects the metacone and what he considers the rudiment of a mesoloph. This low ridge is not present in the Princeton specimen. The presence of this ridge would seem to us to demonstrate that the entire assemblage is a metaloph, which would disprove Lavocat's assertion that this ridge strengthens the evidence for the existence of a mesoloph.

The isolated left upper molar, PU no. 20982 (Fig. 5A), is probably LM^1 rather than LM^2 because (by comparison with Hoffstetter and Lavocat, 1970: 173, Fig.) the relationships of the three measurements are closer to those of M^1 than to those of M^2. Moreover, Lavocat's illustration of the type (1976: Pl. 1, Fig. 5) shows a complete metaloph on M^2 and an interrupted one on M^1. The Princeton tooth is clearly a molar because of the wear facet on the anterior face (Fig. 5B). The width of the posterior half (Table 2) shows that it cannot be M^3. The absence of a wear facet on the posterior face is because this tooth was newly erupted at the time of its owner's death, and the next succeeding tooth had not yet come into contact with it. This tooth is less worn than any tooth figured by Hoffstetter and Lavocat (1970) or by Lavocat (1976), and clearly shows (Fig. 5A) the unworn pattern, essentially as described in the previous paragraph.

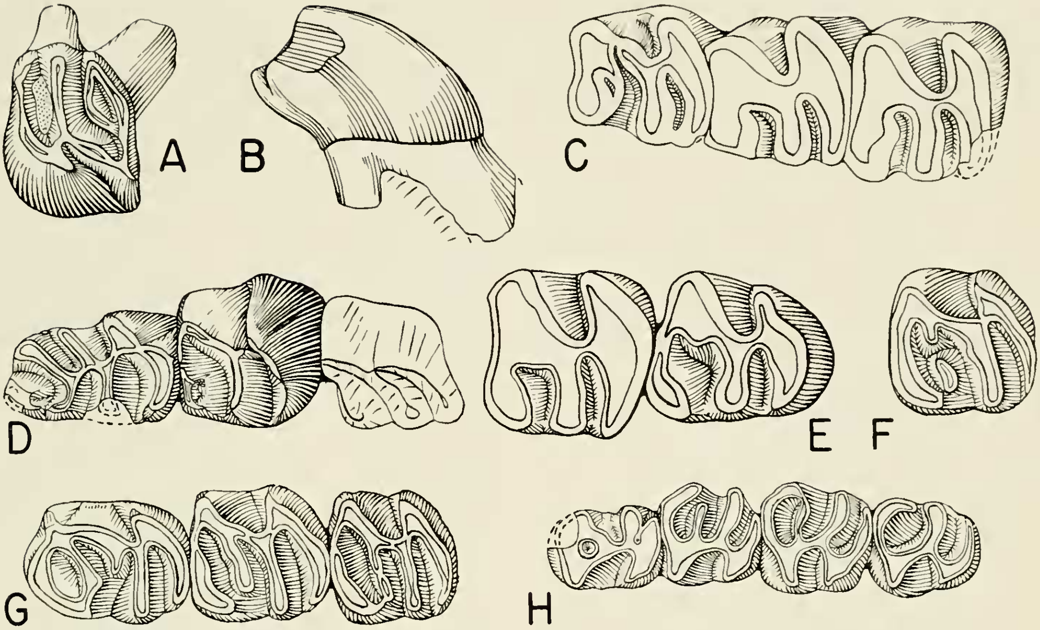

Figure 5. Cheek teeth of *Sallamys pascuali*, *Protacaremys prior*, and *Prospaniomys priscus*. H., ×5; others, ×10. A–B. *Sallamys pascuali*, PU no. 20982, LM^1. A. Occlusal view. Dotted area is matrix. B. Anterior view, showing unilateral hypsodonty. C. *S. pascuali*, PU no. 20907, RP$_4$–M$_2$. D. *S. pascuali*, PU no. 20909, Rdm$_4$–M$_2$. Unerupted M$_2$ with no enamel cap or, at most, an incomplete one. Grooves are in dentine. E. *S. pascuali*, PU no. 21727, RM$_{2-3}$. F. *Protacaremys prior*, FMNH no. P 13295, RM$_1$. G. *Protacaremys prior*, AMNH no. 29707, Rdm$_4$–M$_2$. H. *Prospaniomys priscus*, AMNH no. 29697, Ldm$_4$–M$_3$.

There are only four crests, with not the slightest suggestion of a fifth. The third (the metaloph) is firmly attached to the posteroloph and isolated from the hypocone, although there is a crestlet from the hypocone, running posteriorly across the mesoflexus, at right angles to the direction of what Lavocat (1976: 30) described as a rudimentary mesoloph. The tooth is supported by three roots, two buccal and one lingual. The lingual side of the tooth has about twice the height of the buccal.

The last two upper molars are not represented in the Princeton collection. The published figures and description show that the third loph, the metaloph, has the usual attachment to the mure, and, surprisingly, that the hypoflexus of M^2 was converted by wear to a hypofossette earlier than on M^1. Evidently there was individual variation in depth of flexus as well as in angle of wear.

The last upper molar, as figured by Lavocat (1976: Pl. 1, Fig. 5) seems to us to have a structure completely homologous to that of the anterior molars, with a complete metaloph followed by a complete posteroloph. The latter bends toward, but does not reach, the metaloph. This identity of structure among the molars seems to us clearly to demonstrate the accuracy of our interpretation. We continue to feel that there is no possible basis for assuming, as does Lavocat, that the four-crested upper teeth of *Sallamys* can be interpreted as "structures pentalophodontes" (Lavocat, 1976: 30).

Lavocat's discussion of Wood's interpretation of the crests in *Sallamys* (Lavocat, 1976: 30) seems rather confused, since he comments on the crest considered by Wood to be the mesoloph. But Wood (1974b: discussion, Fig. 1) clearly indicated that, in his opinion, there is no mesoloph in any caviomorph, a position that we still maintain.

Lavocat (1976: 31) stated that the large size of the protocone and small size of the hypocone of the upper molars of *Sallamys* is a primitive condition, "plus proche du plan trigonodonte" than are the teeth of *Platypittamys*. We disagree with this conclusion; none of the Caviomorpha are very close to the trigonodont condition. The rodents that invaded South America must, we feel, already have had a well-developed hypocone. The difference in size of the protocone in *Sallamys* and *Platypittamys* arises from the greater lingual hypsodonty (an advanced character) of the former, which would permit a rapid enlargement of the protocone with wear. How this would occur is clearly shown in Fig. 5A.

According to Lavocat (1976: 31), "le sinus interne des molaires se ferme lingualement, avec l'usure, alors que les vallées externes sont encore bien ouvertes labialement." However, his stereophotograph of the type (1976: Pl. 1, Fig. 5) shows that there is no sequence of closure of the valleys that is consistent from tooth to tooth, and it seems evident that there is great individual variation both in the openness of the hypoflexus, paraflexus and metaflexus (see, for example, Fig. 5A, metaflexus) and the angle at which the wear surface cuts the teeth. This latter is highly variable because of the lingual hypsodonty, which resulted in rotational eruption of the upper teeth, albeit less pronounced than in *Incamys* (see below, pp. 416–418).

As Hoffstetter and Lavocat stated, the talonid of P_4 is completely molariform; a hypolophid as large as those of the molars is present, its lingual extremity joining the posterolophid to isolate a metafossettid. We have previously been in some doubt as to the identification of the posterior lophid of P_4 of echimyids and octodontids, and have tentatively identified it as the serial homolog of the molar hypolophid (Wood, 1949; Wood and Patterson, 1959: 307). Whatever the situation may be in the previously described forms, it would seem that, in *Sallamys* at least, the posterior crest should be called the posterolophid.

The above-cited molarization of the talonid is an advanced character for a Deseadan octodontoid; neither *Platypittamys* (Wood, 1949: Fig. 3C–D) nor *Deseadomys arambourgi* (Wood and Patterson, 1959: Fig. 5A) shows any trace of it. Anteriorly, in the type of *Sallamys pascuali* (Lavocat, 1976: Pl. 1, Fig. 6), the rather stout metaconid has not quite fused with the protoconid, and a short metalophid spur (identified by Lavocat, 1976: 31, as more probably a mesolophid) projects posterolingually from the protoconid; the whole is rather similar to the trigonid area of *D. arambourgi*. In the somewhat more worn PU no. 20907 the protoconid and metaconid are united, but the metalophid spur is still clearly visible, running to the posterior margin of the protoconid (Fig. 5C). The position and relationships of the crest in this tooth seem to us to demonstrate that it cannot be a mesolophid. With a little more wear, this crest would lose its identity, and the tooth would become almost wholly molariform. The ectolophid bears an enlargement that looks somewhat like, but is not, a mesoconid (Fig. 5C). This feature is not present in P_4 of the type (Lavocat, 1976: Pl. 1, Fig. 6).

The lower molars are rather simple in structure, consisting of three essentially transverse lophids (the antero-, hypo-, and posterolophids) separated by deep meso- and metaflexids, and of anterolabially directed, moderately acuminate protoconid and hypoconid separated by a deep hypoflexid (Fig. 5C–E). This last is by far the deepest of the folds, but, due to the oblique manner of wear, all three folds were evidently obliterated at about

TABLE 2. MEASUREMENTS, IN MM, OF TEETH OF *Sallamys pascuali*.

	Lower teeth										
PU nos.	20907 R	20908 R	20909 R	20910 R	20911 L	20912 L	20913 L	21727 R	21950 R	N	$\bar{X}$
P_4–M_3 anteroposterior								8.70		1	
P_4 anteroposterior	1.92		d2.32							1/1	
width metalophid	1.41		d1.21							1/1	
width hypolophid	1.84		d1.47							1/1	
M_1 anteroposterior	1.84	1.92	1.89	1.98		2.00			2.10	6	1.96
width metalophid	1.87	2.01	1.69	1.88		2.03			1.97	6	1.91
width hypolophid	1.97	1.96	2.03	2.06		2.15			2.20	6	2.06
M_2 anteroposterior	1.81	ca. 2.0	ca. 1.9		1.93	2.14		2.17	2.38	7	2.05
width metalophid	2.22				ca. 2.3	2.32		2.18		4	2.24
width hypolophid	2.21				ca. 2.4	2.39		2.21	2.48	5	2.34
M_3 anteroposterior								2.39		1	
width metalophid								1.98		1	
width hypolophid								1.74		1	
I_1 anteroposterior		1.66	1.13			1.53	1.16	1.73	1.51	6	1.45
transverse		1.07	0.75			1.04	0.77	1.27	1.07	6	1.00
ratio		.62	.67			.68	.66	.73	.71	6	.68

Upper teeth				
PU no.	20906 R	PU nos.	20906 R	20982 L
P^4 anteroposterior	1.45	M^1 anteroposterior	1.88	1.84*
width protoloph	2.12	width protoloph	2.65	2.33*
width metaloph	2.04	width metaloph	2.21	2.22*

d = deciduous tooth (dm_4).
* possibly M^2.

the same time, the occlusal surfaces ending up as featureless quadrangles surrounded by a continuous wall of enamel. Even in the highly worn teeth of PU nos. 20908 and 20911, the anterior enamel, although greatly thinned by interdental wear, is still continuous across the front of the tooth. An unworn M_1 (PU no. 20909, Fig. 5D) shows that there was no trace of anything that could possibly be imagined as a mesolophid; that all crests were thin and continuous upon eruption; and that there are minute irregularities, which can only be vestiges of the posterior arm of the metaconid, near the center of the upper half of the posterior face of the anterolophid. This seems to show on M_3 of the type (Hoffstetter and Lavocat, 1970: 173, Fig.; Lavocat, 1976: Pl. 1, Fig. 6), but to have been eliminated by wear on M_3 of PU no. 21727 (Fig. 5E). M_3 narrows posteriorly.

An unerupted M_2 is present in PU no. 20909. It lacks the entire enamel cap, and shows the tooth pattern only in dentine. The pattern seems to have been identical to that of M_1 of the same specimen (Fig. 5D), and again there clearly was no mesolophid. There is a series of radiating furrows in the dentine, which may have marked the attachment of the enamel cap, or which may be shrinkage cracks in the dentine. More worn specimens of M_2 (Fig. 5C,E) likewise show a pattern indistinguishable from that of M_1.

The incisor in PU no. 20913 (Fig. 4F) is crowded against the posterior root of M_2, and the curvature is such that the crowding would have been even greater beneath M_3. This is confirmed by the edentulous fragment of a left ramus, PU no. 20913, in which the roots of M_3 are small, crowded and exceedingly short, because of interference by the incisor.

These observations suggest that M_3 may have been very variable in this species, and in process of reduction.

A little worn, essentially complete dm_4 is present in PU no. 20909 (Fig. 5D); it is a complex tooth. Appreciably longer than any of the molars, it tapers forward rather rapidly. The trigonid and talonid slope down toward the ectolophid, which is worn. A possible explanation of this state of affairs, unusual in so lophate a rodent tooth, is that dm^3 was present, as in *Incamys* and *Branisamys*, and that this tooth and dm^4 formed a wedge when newly erupted, with dm^3 opposing the anterior third of dm_4, and dm^4 opposing the posterior two thirds. There are two buccal, one anterobuccal and two lingual flexids. The identities of the various lophids separated by these flexids (and hence those of the flexids) can be determined by comparison of dm_4 in various Deseadan and Colhuehuapian caviomorphs, as discussed below (pp. 500–501). The talonid is molariform. The large hypoconid was separated by notches from the posterolophid and hypolophid when the tooth was freshly erupted, to judge from its very constricted connections in the specimen. The metaflexid is large and deep, and would convert to a fossettid with extreme wear. Anterior to the point of divergence of the transverse hypolophid, the sinuous, centrally situated ectolophid gives off a labially directed lophid that parallels the angulate labial extension of the hypoconid. The deep flexid between them is the hypoflexid, and the anterior lophid is probably the serial homolog of the molar crest between protoconid and ectolophid that has here parted company with the protoconid. The flexid between this neomorph labial lophid and the protoconid is also a neomorph; it is a little shallower than the hypoflexid, and a minute cuspule is situated at its buccal extremity, probably a remnant of the ancestral marginal crest in this area. Immediately anterior to the point of junction with this neomorph labial lophid, the ectolophid runs anterointernally to fuse with one crest running posterointernally from the protoconid and with another shorter one running posteroexternally from the metaconid. The latter is the serial homolog of the metalophid, while the former is what we have elsewhere (Wood and Patterson, 1959: 288) called the neolophid. The anteroconid is a large cusp that still retains much of its individuality. A slight notch separates it from the metaconid, a much deeper one from the protoconid, and there is a posterior extension, directed toward the ectolophid, which may be the initial stage in a connection of the anteroconid with this crest. The anterolabial flexid, lateral to the anteroconid, deepens toward the center of the tooth, and would presumably convert to a fossettid at a late stage of wear.

The lower incisor extends back to a point slightly behind and pressed against the roots of M_3. Anteriorly, it lies mesiad of the roots of the cheek teeth (Fig. 4D), and is oriented in the usual rodent manner, with the enamel cap (=anterior face) down. However, farther back the tooth rotates (Fig. 4E) so that, beneath the rear of M_2 or the front of M_3, the incisor is twisted, with the enamel cap directed mesiad. Where this takes place, the tooth presses against the posterior root of M_2 (Fig. 4E) and all three roots of M_3 (PU no. 20913), greatly reducing their lengths. The incisor is rather small (Table 2), slender and oval in outline, the posterior portion being very little narrower than the anterior face. The anterior face is smooth and gently convex (Fig. 4E–H). The enamel extends over approximately half of the lateral face and over about a third of the medial. Unfortunately, it was impossible to obtain measurements of the rear end of the incisor of the juvenile PU no. 20909, due to breakage, so that we have been unable to determine the rate of diametric growth of the tooth.

Relationships. As we have previously stated (1959: 300), the Deseadan members of the Octodontidae and Echimyidae are very similar to each other in molar structure, and are separated formally only because their descendants diverged. From the Colhuehuapian on, the two families are distinguished by the retention of dm_4^4 in the Echimyidae and their replacement, ontogenetically, by P_4^4 in the Octodontidae. So far as known, there was no retention of dm_4^4 in Deseadan echimyids. Of the molar characters that we previously gave as separating the earlier members of the two families, *Sallamys* agrees with octodontids in two: the decidedly transverse alignment of the lophs and lophids and the width/length relationships. It agrees with echimyids in the somewhat deeper flexi and flexids and most importantly, in the loss of the metalophids. In this feature *Sallamys* is almost as advanced as *Deseadomys loomisi*, more advanced than *D. arambourgi*, *Xylechimys*, or the Colhuehuapian *Protacaremys* (Fig. 5F–G), *Prospaniomys* (Fig. 5H), and *Protadelphomys*. Loss or interruption of the metalophid is very rare in the molars of the earlier octodontids. Out of a rather large series of the Santacruzian *Sciamys principalis* in the Ameghino collection, only two show metalophid irregularities (MACN nos. A 1886 and A 4113). We therefore conclude that this last feature is the most critical one so far recognized for separating the Echimyidae and Octodontidae during the Deseadan, and hence refer *Sallamys* to the Echimyidae with some confidence. Lavocat recognized the similarity of the Deseadan echimyids and octodontids, and thought that "il s'agit pratiquement ici de saisir la séparation entre deux rameaux issus d'une même souche . . ." (1976: 72). He concluded (1976: 73) that there are many reasons for placing *Sallamys* in the Octodontidae; that it is by no means evident that the octodontids and echimyids were as clearly separable in the Oligocene as we had indicated (we think we made it clear in 1959, pages 300 and 389, that the Deseadan members of the two families were very closely related); and that he left *Sallamys* in the Echimyidae because Wood (1974b: 26) had so placed it and the evidence for shifting it to the Octodontidae was not conclusive. The two molar characters in which *Sallamys* agrees with the earlier octodontids (but also, it may be noted, with some Recent heteropsomyines) should no longer be considered as having diagnostic significance. As an aside, this is an argument against strict numerical taxonomy.

Hoffstetter and Lavocat (1970: 174) see a resemblance to *Paraphiomys* in the lower molars of *Sallamys*. This exists, but is completely offset by the wholly different dm_4 in *Paraphiomys pigotti* and *P. stromeri* (cf. Fig. 5D and Lavocat, 1973: Pl. 26, Figs. 7–10) as well as in the Fayum *P. simonsi* (Wood, 1968: Fig. 5F), transferred below (p. 520) to *Neosciuromys*. Furthermore, it must be noted that these species of *Paraphiomys*, like all the Petromuridae, have a cingulum anterior to the protoconid of the molars, a feature lacking in caviomorphs (see p. 496). As indicated below (p. 521), we retain *Paraphiomys* in the Petromuridae, rather than place it, as does Lavocat, in the Thryonomyidae.

Within the Echimyidae, *Sallamys* appears to fit rather comfortably into the Heteropsomyinae (Fig. 6), displaying, incipiently at least, a number of the molar characters of that group (Patterson and Pascual, 1968: 6). It differs from the Adelphomyinae in the more transverse lophs and lophids and a greater degree of unilateral hypsodonty, and from *Prospaniomys*, the earliest member of the Myocastorinae (if Patterson and Pascual were correct in deriving *Myocastor* from the *Spaniomys* group of echimyids), in the loss of the metalophids and the more complex dm_4 (cf. Fig. 5D,H).

In their definition of the Adelphomyinae, Patterson and Pascual (1968: 5) stated that there was "no unilateral hypsodonty." This is true of the later forms, but

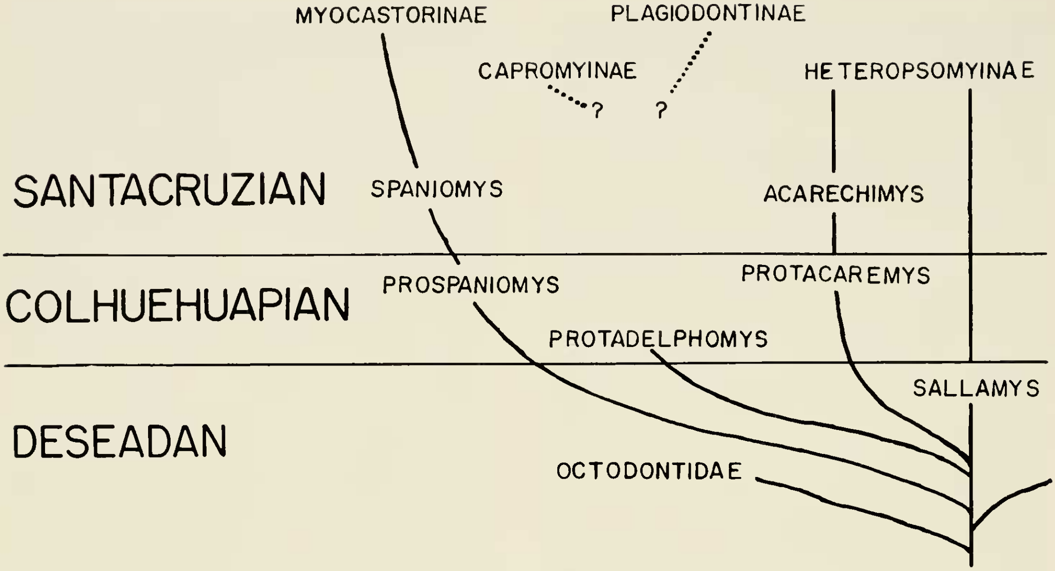

Figure 6. Phylogeny of the early Echimyidae.

the earliest, *Deseadomys*, shows some degree of it in the upper teeth. The statement should be amended to read: "slight initial unilateral hypsodonty, not subsequently increasing."

Sallamys displays no detectable tendencies toward the types of molar structure encountered in the Echimyinae and Dactylomyinae, subfamilies so far unrepresented, or at any rate unrecognized, in the Tertiary.

The Colhuehuapian *Paradelphomys* (Patterson and Pascual, 1968: Fig. 3) shows some resemblances to the dactylomyines in the obliquity of the lophids, the isolation of the posterolophid, the extension of the mesoflexid nearly to the anterior extremity of the tooth, and the simple trigonid of dm_4. Whether or not this is in any way indicative of affinity is at present quite uncertain and will remain so until later Tertiary dactylomyines are discovered. The possible relationships are suggested in Fig. 6.

On the basis of the few early forms then known, we tentatively sketched a phylogeny of the Echimyidae (1959: 302, Fig. 3) that suggested an early dichotomy into Adelphomyinae and the ancestry of the remainder of the family. The discovery of *Sallamys* suggests that this may have been an oversimplification, and that the actual situation was even more complex than we had supposed. *Sallamys* is about as advanced in molar structure as is *Deseadomys*, although in somewhat different ways, and is less advanced in the premolar. It is even more advanced over the later *Protacaremys* and *Prospaniomys* as regards crown height and metalophid reduction, and possesses a much more complex dm_4 than does *Prospaniomys* (cf. Fig. 5D,H). It is more advanced than the poorly known Colhuehuapian *Protadelphomys* in metalophid reduction and than *Paradelphomys* in lower milk molar complexity.

As pointed out below (p. 501), the adelphomyines and the *Spaniomys* group have a relatively simple dm_4, comparable to those of octodontids, whereas the known heteropsomyines have a complex dm_4 nearly comparable to that of *Cephalomys*. The latest Pleistocene or early Recent Antillean heteropsomyines have a simple dm_4, which suggests either that

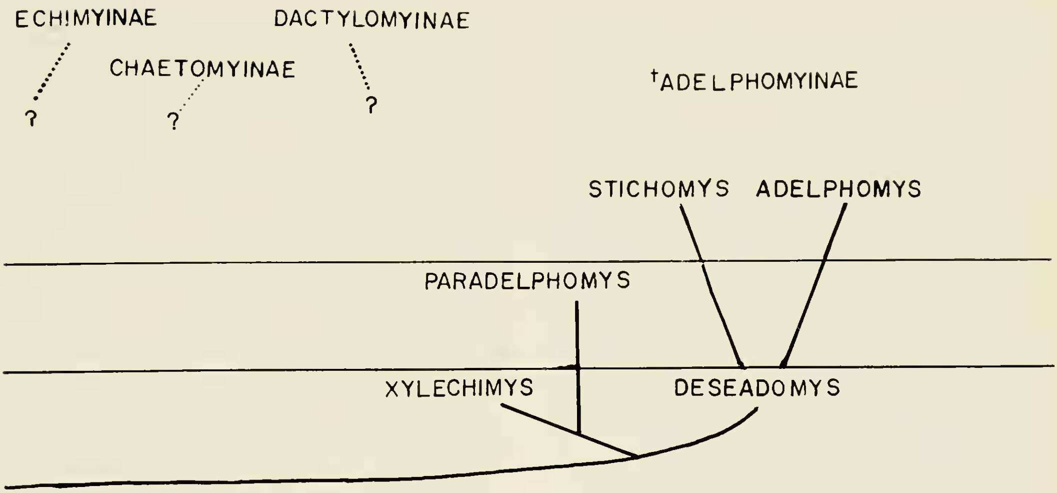

Figure 6. Continued.

not all early members of the subfamily had a complex one, or (a less probable hypothesis) that secondary simplification occurred in the ancestry of these forms.

We interpret these bits of evidence to mean that the heteropsomyines began their radiation at least as early as did the adelphomyines, and that the *Spaniomys* group may well be of equal antiquity and not an offshoot from the Heteropsomyinae, despite the close similarity between *Protacaremys* and *Prospaniomys* in molar structure.

Sallamys cannot have been ancestral to any Colhuehuapian or Santacruzian heteropsomyine now known. With a few easily made mental rearrangements of crests and valleys it would be possible to visualize it as being in or near the ancestry of various later forms, but in the absence of known intermediates such exercises would be vain and probably misleading. There is a resemblance, however, between *Sallamys* and *Chasichimys* of the Arroyo Chasicó (Pascual, 1967).

Due to conservative inertia as much as anything else, we have hitherto maintained the Capromyidae as a distinct family descended from the Echimyidae. Morphologically, this is not really justified, and, in general agreement with authors such as Ellerman (1940), we now place the two Antillean subfamilies Capromyinae and Plagiodontinae in the mainland family. Patterson and Pascual (1968:1, n. 2), in commenting on this possibility, stated that the subfamilies of the Echimyidae and Capromyidae would in that case become tribes. We do not take this step here because the capromyines and plagiodontines, while agreeing in possessing hypselodonty (the capromyine *Hexalobodon* alone excepted) and cement, differ in cheek tooth structure quite as much as do the other subfamilies. Their divergence, if they diverged from a common stock, may or may not have taken place in the Antilles; these subfamilies may or may not be relict survivors of the original caviomorph migration to South America (see below, p. 456); at present there is no evidence that bears on these questions.

The occurrence of macroscopic deposits of cement is sporadic in the Caviomorpha—as in rodents generally—and is not necessarily indicative of higher affinities. In addition to the above-mentioned Antillean forms, it is present in the Deseadan *Litodontomys*, in its possible relative the Santacruzian *Olenopsis*, in chinchillids from the Deseadan on, in later eocardiines and in caviids and hydrochoerids, and in Pliocene and later octodontids, abrocomids, myocastorines and dinomyids. A thick deposit of cement is merely an enlargement of the universally present microscopic layer of cement that covers unerupted mammalian teeth, and is associated with hypsodonty and hypselodonty in rodent lineages in which the other components of the cheek teeth are either separated or only narrowly connected.

The peculiar genus *Chaetomys* is nowadays universally accorded a subfamily of its own, usually in the Erethizontidae. There have been few informed comments on the taxonomic position of this subfamily, due to the rarity of specimens of *Chaetomys*. Through the kindness of Dr. Paulo Emilio Vanzolini, one of us (B.P.) recently had the opportunity to examine a skeleton of *Chaetomys subspinosus* in the MZUSP.

If one looks mainly, or only, at the structure of the feet, placing the Chaetomyinae in the Erethizontidae is a logical step, the resemblance between the two groups in this respect being strikingly close. The cheek teeth of *Chaetomys*, however, are very different in structure from those of the erethizontids. On the basis of tooth structure, Schaub (*in* Stehlin and Schaub, 1951: 369) placed *Chaetomys* in the Echimyidae, following Miller and Gidley (1918: 445) who, however, as usual, gave no reasons for their action. Later (1958: 742), Schaub placed *Chaetomys* in the echimyid subfamily Echimyinae along with *Heteropsomys* and *Spaniomys*, as opposed to the only other subfamily he listed, the Dactylomyinae, again stressing the cheek-tooth structure.

This familial assignment is strongly supported by two characters that we regard as fundamental, both of them strongly negative as regards erethizontid affinities and one strongly positive as regards echimyid ones. In contrast to the known erethizontids and in agreement with all other living caviomorphs, *Chaetomys* lacks a posterior carotid foramen, and hence an internal carotid artery. Ellerman (1940: 175, Fig. 42) shows what could be interpreted as a small foramen anterointernal to the foramen lacerum posterior. In the MZUSP skull there is a depression in this area that does not communicate with the cranial cavity. Retention of this artery is a basic character of the New World porcupines, as Bugge (1974a: 71; 1974b: 70) has recently stressed. In agreement with all post-Deseadan echimyids and in contrast to all other caviomorphs, dm_4^4 are retained throughout life. There can be no doubt of this in the specimen of *C. subspinosus* examined (MZUSP unnumbered). The anterior cheek teeth are lower in crown height than are the first molars, and the flexi and flexids are more nearly obliterated, both features being due to wear. They were clearly the first of the series to have erupted, and X-rays have revealed no trace of replacing teeth beneath them. We believe reference of the Chaetomyinae to the Echimyidae to be fully justified.

With this transfer of *Chaetomys*, the Erethizontidae becomes a very compact group, and the Echimyidae an even more complex one. However, the Echimyidae now include all caviomorphs in which dm_4^4 are retained.

As a subfamily of the Echimyidae, the Chaetomyinae may be defined as follows: cheek teeth generally resembling those of the Echimyinae, but uppers with five lophs, metaloph forming an independent central crest; malar robust, very deep anteriorly, with large postorbital process nearly meeting well-developed postorbital process of frontal, and with little or no trace of jugal fossa on lateral surface; parietal crests well developed, only slightly convergent posteriorly; bulla with prominent porus acusticus externus directed anteroexternally; paroccipital process blunt, barely projecting; coronoid process of mandible greatly reduced; feet erethizontid-like.

Our present very tentative concept of echimyid phylogeny is summed up in Fig. 6. For so long as five of the eight subfamilies are unknown or unrecognized in the Tertiary, matters will remain in an unsatisfactory state; the evolution of all five may well have gone on for the most part in the northern half of the continent or (for the Capromyinae and Plagiodontinae) in the Antilles. Our placing of the Dactylomyinae next to the Adelphomyinae rests on nothing more than the few resemblances between the living forms and *Paradelphomys* noted above (p. 392); these hardly constitute compelling evidence. Whether or not the Echimyinae arose from or had a common ancestry with the Heteropsomyinae is wholly conjectural. The placement of the Capromyinae next to the Myocastorinae rests on somewhat firmer ground. The two groups have long been associated by a number of authorities, usually in a family of their own. George and Weir (1974: 102) conclude that on karyotypic evidence the two groups are closely related, more closely than either is to the heteropsomyine *Proechimys*, the only other echimyid whose karyotype was known to them. Woods (1972: 189) reported that myological evidence does not permit a decision as to whether *Myocastor* is an echimyid or an octodontid (dental evidence clearly favors echimyid affinities). Gorgas, in a comparative study of the rodent stomach and alimentary canal (1967: 367), has found that *Myocastor* and the capromyines stand apart from other echimyids—and also from each other—in some features. It seems to us that all this is not incompatible with an early origin of myocastorines from the basal echimyid stock, with the capromyines perhaps arising from some member of the myocastorine group. The position of the Chaetomyinae within the family is even more problematical than that of the other subfamilies.

Superfamily CAVIOIDEA Kraglievich 1930b

Series B. DASYPROCTIDAE, DINOMYIDAE and CUNICULIDAE (pp. 511, 523)

Family DASYPROCTIDAE Smith 1842

Incamys Hoffstetter and Lavocat 1970

Emended Diagnosis. Skull basically dasyproctid, with large orbits and bullae; snout elongate, ventral side horizontal; anterior part of fossa of origin for *M. masseter medialis* weakly marked, posterior part deep and corrugated; nasals parallel-sided, tubular anteriorly; large interpremaxillary foramen; incisive foramina enormous, elongate and laterally expanded; lateral wall of nasolacrimal canal very thin; interorbital fenestra between frontal and maxillary; anterior suture of malar with maxillary straight; no postorbital process or jugal fossa on malar; orbitosphenoid large, quadrate; no separate interparietal; mastoid continuous with bulla, inflated and septate; large fenestra between presphenoid and palatine, opening into orbitotemporal fossa; dental formula I_1^1 P_1^1 M_3^3, dm_1^2; incisors slender, proportionately small; cheek teeth tetralophate, marked lingual hypsodonty in uppers; anteroloph fully separate in earliest stages of wear, becoming joined with paracone buccally; other lophs unite early and converge posterointernally on hypocone; posterolophid isolated in early stages of wear of lower teeth; other lophids unite early and converge anteroexternally on protoconid; metalophid short, connected to protoconid.

Type Species. Incamys bolivianus Hoffstetter and Lavocat 1970.

Distribution. Deseadan Oligocene, Bolivia and Patagonia.

Incamys bolivianus Hoffstetter and Lavocat 1970
Figures 7–19

Incamys bolivianus Hoffstetter and Lavocat 1970: 173, Fig.; Lavocat, 1976: 50–54; Pl. 3, Figs. 1–7; Pl. 4, Figs. 1–3, 7.

Synonym. Incamys pretiosus Lavocat 1976: 54–59; Pl. 4, Figs. 4–6; Pl. 5, Figs. 6–7; Pl. 6, Figs. 3–5.

Diagnosis. As for the genus. Tooth measurements as given in Tables 3–4. The statistics seem to us to demonstrate that our sample represents a single variable species.

Type. Anterior portion of the skull, back as far as M^3, with associated left ramus, including a complete set of upper and lower cheek teeth, deposited in Muséum Nationale d'Histoire Naturelle, Paris; cited without identifying number by Hoffstetter and Lavocat (1970: 173) and without museum identification as SAL 117A (skull) and SAL 117B (ramus) by Lavocat (1976: 50).

Synonymized Species. Lavocat (1976: 54) described a second species of *Incamys, I. pretiosus,* which he differentiated from the genotypic species only by saying "molaires supérieures sans mésolophe, métalophe développé." If we are correct in not recognizing a mesoloph in any caviomorph, this becomes a meaningless distinction. Hoffstetter and Lavocat (1970: Fig.) and Lavocat (1976: Pl. 4, Figs. 1, 3) show the metaloph in *Incamys* either joined to (M$^{1-3}$) or about to join (P^4) the combined protoloph and mure. In only one (PU no. 20963, Fig. 17F) of the 50 specimens of upper cheek teeth in the Princeton collection does the metaloph do this, although in some other specimens it might make such a junction with further wear (Fig. 17D). Lavocat's specimens that he referred to *I. pretiosus* (1976: Pl. 4, Fig. 4; Pl. 6, Fig. 3) agree with the majority of our specimens. There is very considerable variability in all of the teeth of *I. bolivianus*, a point concurred in by Lavocat (1976: 46), enough so that we at first suspected the possibility of there being two species at Salla, but which we now feel means that there was only a single, highly variable species. Certainly the tooth measurements (Tables 3–4) indicate a high degree of size variability, but it seems to be continuous. It is partly due, as discussed below (p. 416), to the rotational eruption of the teeth, and there does not seem to be any association between size and morphological variants. Lavocat (1976: 41) suggests that there may have been a third species of *Incamys* at Salla, but he gives no data. Assuming that the scale given for Lavocat's stereophotos is accurate, the upper teeth of *I. pretiosus* (1976: Pl. 6, Fig. 3) fall within the size range of those of *I. bolivianus* (Table 3), and their pattern is identical to that here considered to be typical of *I. bolivianus* (Fig. 17B). We therefore conclude that *I. pretiosus* is a synonym of *I. bolivianus*.

Referred material. 140 specimens in the MNHN, Princeton, and MACN collections, listed in Appendix 1, p. 528.

A maxilla, SAL 118, containing RP^4–M^2, differs markedly from all other specimens that have been referred to *Incamys* (Lavocat, 1976: Pl. 4, Fig. 2), and represents, we believe, an undescribed genus, as discussed below (p. 430).

Horizon and Localities. Deseadan, early Oligocene, lower part of Estratos de Salla; Salla-Luribay Basin, Bolivia. PU nos. 20937–40 and 20945–6 are from Tomolo (see above, p. 383, for discussion of Tomolo and Toloma), midway between Salla and Aroma; nos. 20941–3 and 20947–9 were collected in the vicinity of Salla Farm; nos. 20950–2 are from dark red to reddish-brown rocks in the lower part of the Salla succession; nos. 20953–81 were found at Pampa Tapial, in a grayish-white, gypsiferous clay some 10 m above a 30–50 cm thick bed of greenish-gray limestone within an area of 20 by 20 m that also yielded specimens of *Sallamys pascuali.* Nos. 20916–36 and 20949 are without precise locality data. The partial skull, PU no. 20944, was found at locality "V-33," the precise location of which is not known to us (L. Braniša, field notes). MACN no. A 52-113 is presumably from Cabeza Blanca, Chubut, Argentina.

Description. The juvenile Princeton skull has suffered some distortion—partially corrected in the figures—and was enclosed in exceedingly hard matrix,

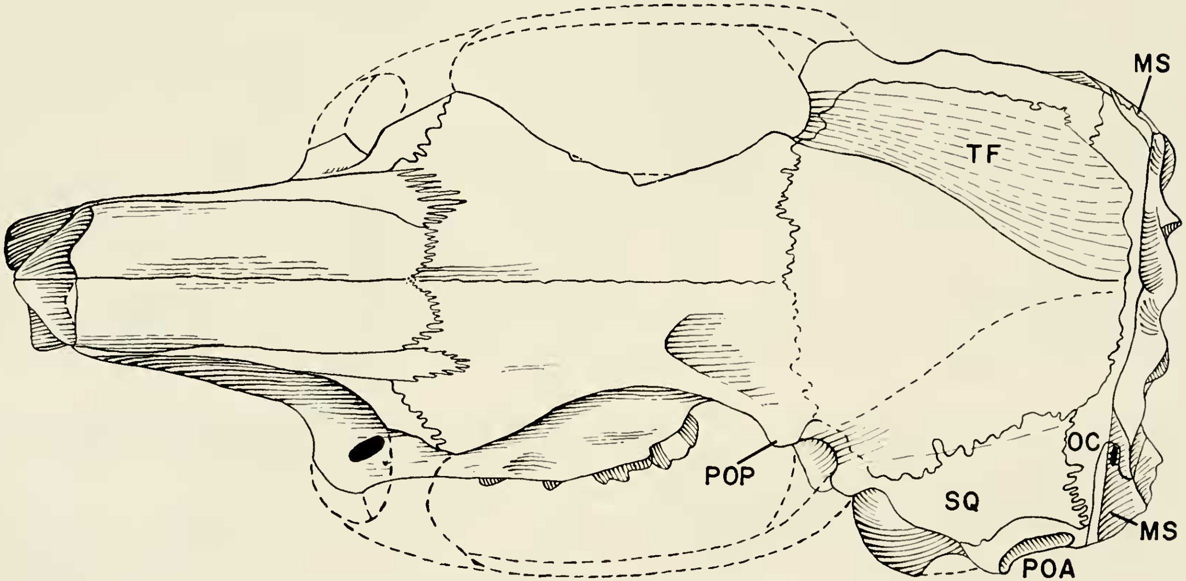

Figure 7. Dorsal view of the skull of *Incamys bolivianus*, PU no. 21726, juvenile, ×3.

Abbreviations: MS—mastoid; OC—occipital; POA—porus acusticus externus; POP—postorbital process; SQ—squamosal; TF—temporal fossa.

which unfortunately tended to be at its hardest along suture lines and around foramina. Removal of all of the matrix has not been possible, with the result that some details are still obscure. The skull of PU no. 21945, however, was in a softer matrix, was less distorted, and has provided an almost complete understanding of the skull structure. Moreover, the facial region (PU no. 20944) supplements the skulls in various features. These three specimens differ somewhat in size, the facial region representing the largest individual. These differences seem to be due to age. The skull of PU no. 21726 is that of an immature animal in which the milk molars are still in place and M^3 has just come into wear. Series of living dasyproctids reveal that skull growth continues until the full adult dentition is in use.

The skull as a whole is strongly arched, agreeing in this with the type (Lavocat, 1976: 57), and is about as in *Myoprocta*, with large orbits and very large bullae. The region in front of the cheek teeth forms approximately a quarter and the region posterior to the front margin of the glenoid cavity approximately a third of the total length (Figs. 10, 12, 14). The skull roof is much flatter transversely than in later dasyproctids, in this respect resembling *Cephalomys*, and is even slightly concave in the nasal and frontal regions. In contrast to other members of the family, there is a marked interorbital narrowing of the dorsal surface of the skull, and the braincase is flatter and relatively wider than in later dasyproctids. The sagittal crest is short and feebly expressed (Figs. 7–8).

The rostrum is moderately long and rather slender, comparable to the rostra of living dasyproctids in general proportions, but less tapering and more nearly parallel-sided, so that the dorsal root of the zygoma stands out about at right angles to the sides of the rostrum (Fig. 8), a resemblance to *Cephalomys*. The ventral profile of the snout is nearly straight, as in living dasyproctids, and there is a suggestion of the characteristic abrupt downturn of the premaxilla immediately behind the incisors (Fig. 10).

The infraorbital foramen is preserved *in toto* only on the right side of PU no. 21945. The foramen was a large, vertically oriented oval, rather different from those of the modern dasyproctids. Because both the dorsal and ventral roots of the lateral wall of the foramen are considerably elongate anteroposteriorly in contrast to the slender central section of the lateral wall, the infraorbital foramen is nearly circular as seen from the side (Fig. 12). The dorsal and ventral roots extend about equally far forward, so that the dorsoventral axis of the foramen would have been vertical, rather than inclined forward as Lavocat believed (1976: 52). There is a prominent elevation (below the ridge that marks the course of the incisor) that occupies part of the ventral border of the masseteric fossa. A similar elevation occurs in living dasyproctids, but not in *Neoreomys*.

The nasals, not preserved in either of Lavocat's partial skulls, are very much longer than in *Dasyprocta* or *Myoprocta*. They extend back to a point above dm^4 in the juvenile or M^1 in the adult, and slightly behind the lacrimal foramen, about as in *Cephalomys* and *Neoreomys*, although their posterior ends are in front of the lacrimal foramen in the Santacruzian genus. Very long nasals are characteristic of the Paramyidae and Reithroparamyidae (Wood, 1962a: Figs. 2A, 13A, 48A) and we accordingly interpret the condition in *Incamys* (and also in *Branisamys*, see below, p. 433) as primitive. *Platypittamys* has somewhat shorter nasals, while those of living dasyproctids are shorter still. The anterior end of each nasal is tubular, the tubular part forming perhaps half the length of the bone. In living dasyproctids, the combined nasals have a tubular anterior end, but there is no groove between the bones as there is in *Incamys* (Figs. 7–9). The nasals of *Neoreomys* are much less tubular than in

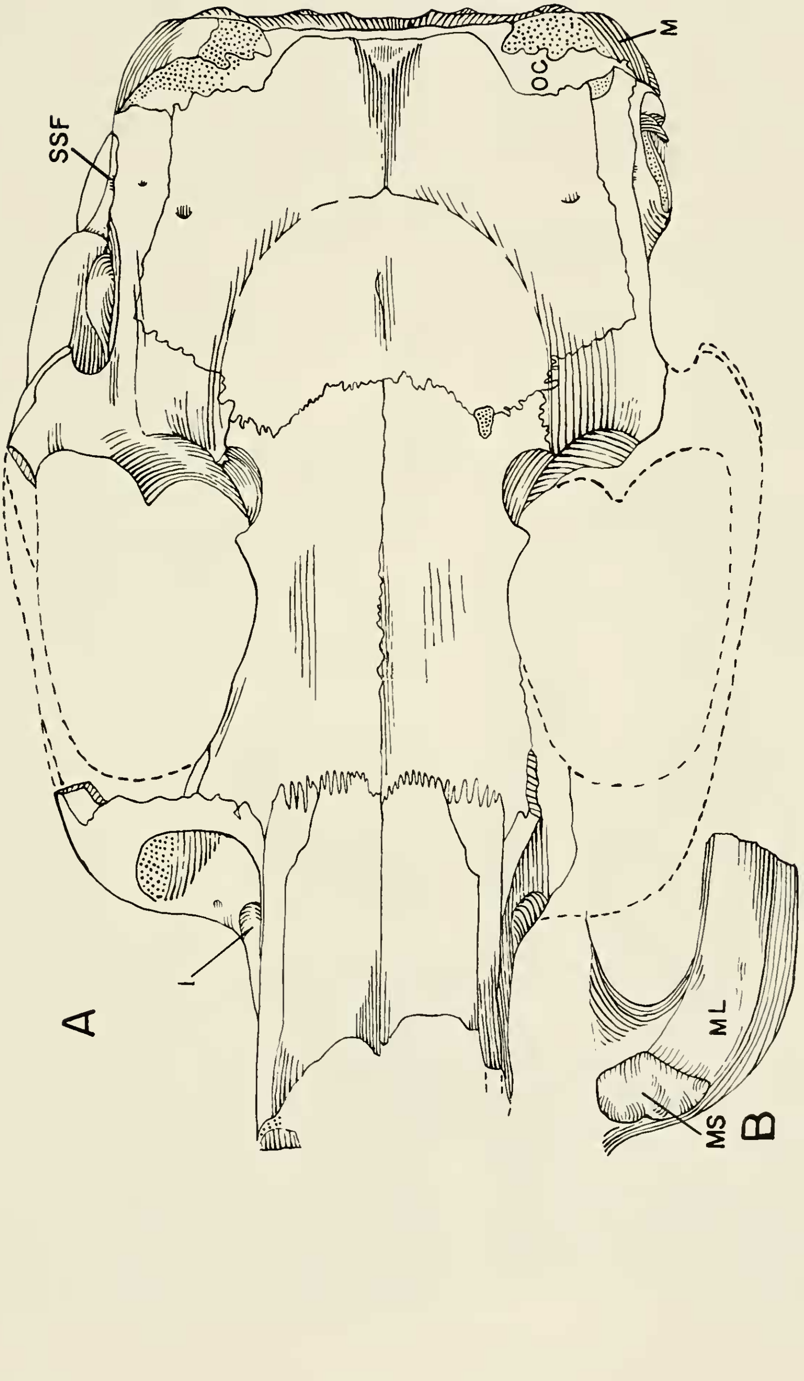

Figure 8. *Incamys bolivianus*, PU no. 21945. A. Dorsal view of skull, ×3. B. Ventral view of anterior part of right zygoma, anterior end to the right. ×5.

Abbreviations: I—base of upper incisor; M—mastoid; ML—fossa for origin of *M. masseter lateralis*; MS—fossa for origin of *M. masseter superficialis*; OC—lateral process of occipital; SSF—subsquamosal foramen.

living dasyproctids. The posterior portions of the nasals in *Incamys* are flattened, even slightly concave transversely. The sides of the bones are nearly parallel, but they are slightly pinched at the middle. The nasals are generally similar in outline to those of modern dasyproctids. The nasofrontal suture bends forward toward the midline, an irregularly pointed process of the frontals separating the posterior ends of the nasals (Figs. 7–9).

The ascending portions of the premaxillaries are long and somewhat expanded at their posterior ends. Their terminations are curiously asymmetrical in two of the three specimens at hand (Figs. 7–9). On both sides of PU no. 21726 they extend back farther than the nasals, whereas only the right one of PU no. 20944 does so. The left premaxillary of the former is of normal shape, but the right in the course of development evidently expanded medially at the expense of the nasal, reaching farther toward the midline and taking over the area occupied on the left side by a small, forwardly extending wedge of frontal. The nasals and premaxillae reach back to the same level in PU no. 21945, and the two premaxillae are symmetrical (Fig. 8A). The fronto-maxillary suture is well in advance of the rear of the nasal and premaxillary, and is not so obliquely inclined as in living dasyproctids and *Cephalomys*. In *Neoreomys* the entire anterior end of the frontal is an essentially transverse line. On the ventral side of the bones, the interpremaxillary foramen is very large in PU no. 20944, much larger than in any other dasyproctid we have seen, being about 1.6 mm in diameter (Fig. 14B); it is relatively smaller, although still large, in the type (Lavocat, 1976: Pl. 3, Fig. 2) and in PU no. 20953, both of which are smaller and younger individuals, and this area is missing in PU no. 21945. It is partially obscured by crushing in PU no. 21726. The size of the foramen is variable in Recent dasyproctids.

On the lateral side, the premaxillary part of the fossa for the origin of *M. masseter medialis, pars anterior* is not so clearly defined as in *Neoreomys* and living dasyproctids, and does not have so large an anterior extension (Fig. 10A), although it is relatively deep dorsoventrally. Lavocat (1976: 51) apparently confused the crest marking the anterior limit of the masseteric fossa (Fig. 10A; AM) with the premaxillary-maxillary suture on the ventral lateral part of the snout. His description of the suture, "elle part de façon rectiligne à 45 degrés vers le haut et l'avant," agrees perfectly with the limits of the masseteric fossa as we indicate them on Figs. 10A and 12, and is very unlike the highly crenulate suture that we show on the same figures. A close examination of Lavocat's excellent stereophoto (1976: Pl. 3, Fig. 1) shows that the suture in this area is still covered by a thin layer of matrix.

A striking feature of the *Incamys* skull is the enormous size of the incisive foramen, which occupies the greater part of the palate anterior to the cheek teeth (Fig. 14A,B). The anterior part of this aperture seems to correspond to the normal rodent incisive foramina, but the posterior part is peculiar indeed. The anterior half of the septum between the foramina is broad and rounded and reaches the level of the palate in the usual manner, but the posterior half is a slender vertical septum that does not reach so far ventrad (Fig. 14B). The premaxillary-maxillary suture reaches the sides of the foramina near the level at which the change in the septum occurs. The apparent difference between the shape of the suture in PU no. 21726 (Fig. 14A) and that in the type (Lavocat, 1976: Pl. 3, Fig. 2) is merely because this area had not been cleared of matrix in the latter. Near the rear of the opening, the ventral margin of the septum is about 3 mm dorsal to the palate (Fig. 14B). None of the available specimens is complete, but by combining them all (Fig. 14A; Lavocat, 1976: Pl. 3,

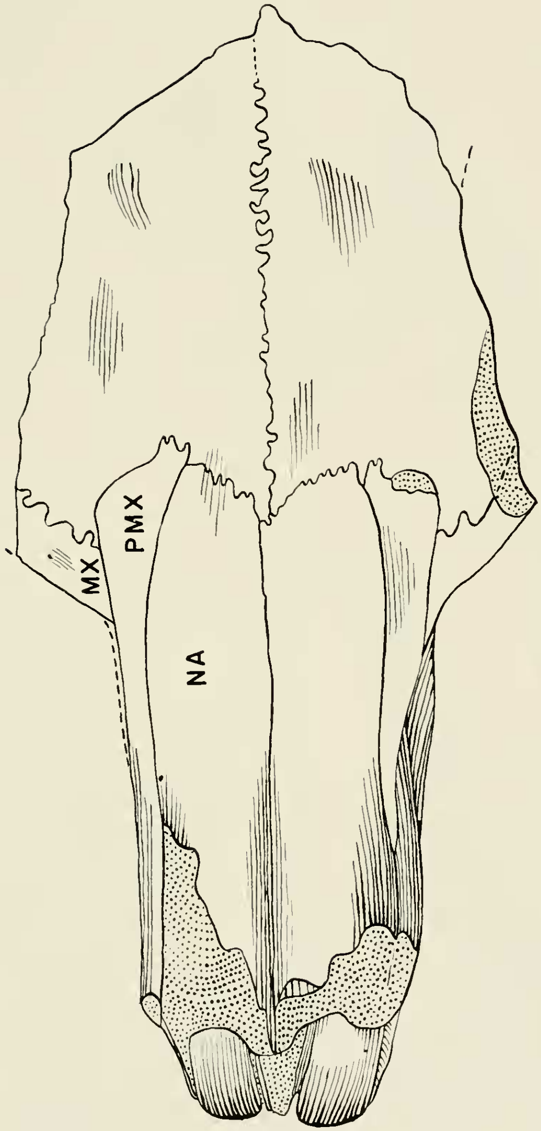

Figure 9. Dorsal view of partial skull of *Incamys bolivianus*, PU no. 20944, ×4.

Abbreviations: MX—ascending process of maxillary; NA—nasal; PMX—premaxilla. Dotted areas are matrix.

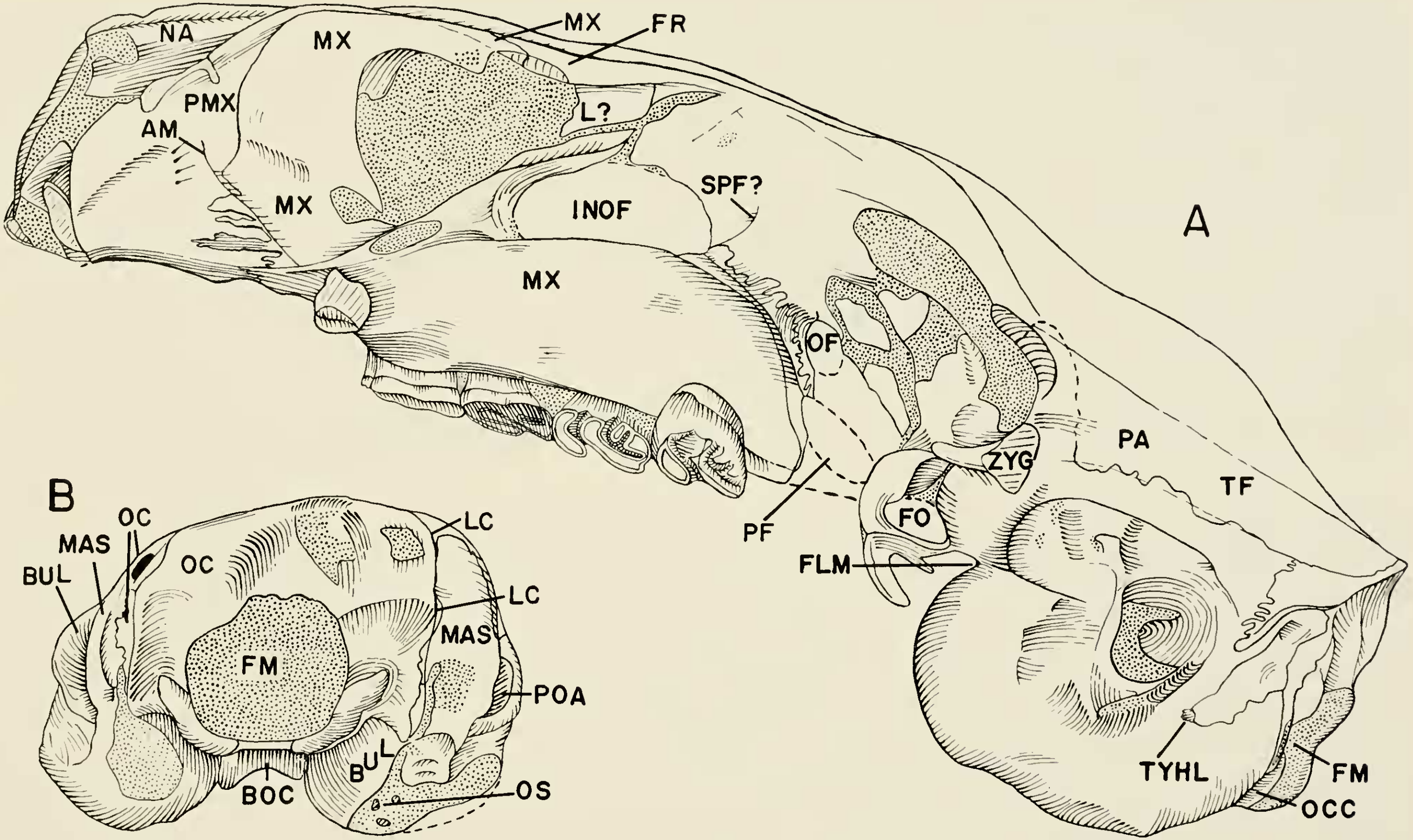

Figure 10. Skull of *Incamys bolivianus*, PU no. 21726, juvenile. Dotted areas are matrix. A. Lateral view, ×4. B. Occiput, ×3.

Abbreviations: AM—anterior limit of masseteric fossa; BOC—basioccipital; BUL—bulla; FLM—foramen lacerum medium; FM—foramen magnum; FO—foramen ovale; FR—frontal; INOF—interorbital fenestra; L?—possibly lacrimal; LC—lambdoid crest; MAS—mastoid; MX—maxillary; NA—nasal; OC—occipital; OCC—occipital condyle; OF—optic foramen; OS—??auditory ossicles; PA—parietal; PF—pterygoid fenestra; PMX—premaxillary; POA—porus acusticus externus; SPF—?sphenopalatine foramen; TF—temporal fossa; TYHL—area of articulation of tympanohyal; ZYG—broken base of zygoma.

Fig. 2) it is clear that, in life, the septum was continuous, as postulated by Lavocat (1976: 51). The maximum width, across both foramina and the septum, is 5.0 mm or perhaps a little more. There is no trace of the premaxillary-maxillary suture on the septum between the incisive foramina in any of the specimens, although in all of them a median suture is discernible. We therefore suspect that all or most of the septum may be composed of the premaxillaries, as in other caviomorphs. Just behind the premaxillary-maxillary suture, on the lateral wall of the fenestra, is what seems to be a large opening, probably the anterior end of the nasolacrimal canal. The incisive foramina are closed posteriorly slightly behind the base of the upper incisors and opposite the middle of P^4, at which point the septum descends abruptly to the ventral margin of the opening.

We have not observed similar fenestrae in any living dasyproctid, in all of which the premaxillary-maxillary suture passes across the palate at the rear of the incisive foramina. However, in known fossil dasyproctids there appears to be a backward expansion of the foramina into the maxillary (*Cephalomys*, Wood and Patterson, 1959: Figs. 21B, 22B; *Neoreomys*, Scott, 1905: Pl. 65, Fig. 1; *Scleromys*, Scott, 1905: Pl. 65, Fig. 13). In *Neoreomys* (PU no. 15572), the suture crosses the middle of the foramina, the posterior part of the foramina being solidly roofed by the maxillae. A posterior enlargement of the incisive foramina is clearly visible in the Santacruzian octodontids *Sciamys* (Scott, 1905: Pl. 67, Figs. 1f, 5a, 6a, 7a) and *Acaremys* (Scott, 1905: Pl. 67, Fig. 4a), and echimyids (Scott, 1905: Pl. 67, Fig. 10a), and also occurs in Recent members of these families and in *Abrocoma*, *Chinchilla* and *Lagidium*. This may be a primitive character for caviomorphs. The octodontids *are* primitive caviomorphs, and it should be noted that the enlargement is present in the North American Uintan franimorph *Protoptychus* (Wahlert, 1973). No trace of an enlargement is present in the Deseadan dinomyid *Branisamys* (possibly indicating an early reduction in the size of the opening in this family); and the two skulls of the primitive caviomorph *Platypittamys* are so preserved as effectually to conceal this area. This region is not preserved in the partial skull of *Sallamys* (Lavocat, 1976: Pl. 2, Figs. 1, 4). The foramina are very short in the snout described by Lavocat as *Luribayomys masticator* (1976: Pl. 5, Fig. 1).

An elongate incisive foramen, apparently extending as far back as the level of the anterior end of the cheek teeth, was present in the early Oligocene African *Metaphiomys* (Wood, 1968: Fig. 6A), where its development was apparently similar to that in *Petromus* (Tullberg, 1899: Pl. 6, Fig. 16). In these forms, however, the incisive foramina are sunk into a palatal depression (Wood, 1968: 51–52) quite different from conditions in most caviomorphs, although there are some similarities to the well-developed gutter that leads back from the foramina in *Neoreomys* (PU no. 15572). The foramen in the African forms is more normal in its shape than in *Incamys* and the Santacruzian octodonts. Such an enlarged incisive foramen is not primitive for rodents (e.g., Wood, 1962a: Figs. 13C, 24C, 48B for paramyids and reithroparamyids; Dawson, 1961: Pls. 2, 3 for *Sciuravus*).

The fossa for the origin of *M. buccinator* extends forward, lateral to the incisive foramina, as far as the premaxillary-maxillary suture, approximately as in *Cephalomys*, *Neoreomys* and *Scleromys*. We disagree with Lavocat's statement (1976: 52) that this fossa is quite different from what is found in other caviomorphs. In living dasyproctids the fossa extends medially almost to the midventral line in adult specimens, the fossae of the two sides being separated only by a narrow ridge. It would seem that the buccinator is a more powerful muscle in *Dasyprocta* and *Myoprocta* than it was in known earlier genera. This suggests the possibility that in the ancestry of these forms the posterior part of the incisive foramina may have become floored by medial extensions of the maxillae that enlarged *pari passu* with the increase in the size and strength of the buccinator muscle in later members of the family.

In the living forms, and even more in *Neoreomys*, the maxillary part of the fossa for *M. masseter medialis, pars anterior*, dorsal to the incisor, is the deepest part. This deepening is present to an exaggerated degree in *Incamys*, where the area seems to be subdivided into a number of subsidiary pockets (Fig. 10). However, the absence of these from both sides of the best preserved skull (Fig. 12) suggests that they may have been formed post-mortem either by crushing or by breaking. The right zygoma is preserved in PU no. 21945, revealing a fossa for the origin of *M. masseter superficialis*, distinct from that of *M. masseter lateralis* (Fig. 8B).

There is a large opening in the maxillary on the dorsal surface of the ventral root of the zygoma (Fig. 7). This, we believe, is too far laterad to be related to the nasolacrimal canal, and we interpret it as a nutritive foramen for the superior alveolar blood vessels (cf. Wood, 1974a: 35). Lavocat (1976: 54) mentioned "un petit foramen qui est sans doute l'entrée du nerf alvéolaire antéro-supérieur." This foramen is faintly visible in his Pl. 3, Fig. 1, where it can be seen to be as large as in the Princeton material.

The orbital portion of the maxillary is arched transversely over the roots of the cheek teeth and does not meet the orbital portion of the frontals above the molars. In PU no. 21726 (Fig. 10A) there is an oval vacuity here in which no trace of bone was present, and in the older PU nos. 20944 (Fig. 11) and 21945 (Figs. 12, 15A) there are corresponding but somewhat smaller openings. Such an opening is likewise present in the type (Lavocat, 1976: Pl. 3, Fig. 1). This is a puzzling feature that seems to have resulted either from a lack of ossification in the ventral part of the frontal or, less probably, from universal post-mortem loss of delicate bone. In living dasyproctids the ventral portion of the frontal is very thin and grows down over the maxillary; union of the two bones is not entirely complete in some of the younger individuals at hand, and in these it is possible to pass a bristle through the skull between the frontal and the maxillary. Since the parts of the frontals bordering these vacuities in the fossils do not show signs of breakage, and since the openings are present in all four specimens (the type skull of *I. pretiosus* would seem, from Lavocat's stereophotos, not to have had this area cleared of matrix), we conclude that the vacuities are natural. We have termed the opening the interorbital fenestra (Figs. 10, 12, 15A; INOF). Lavocat (1976: 52 and Fig. 3; I) identified this opening as the sphenopalatine foramen, an interpretation that seems highly improbable to us, although the foramen possibly is included in the fenestra. What we have identified as the foramen (Fig. 10; SPF) lies farther to the rear. Openings of this nature within the orbit are highly unusual among rodents, but they do occur (e.g., *Myosciurus, Jaculus*; Ellerman 1940: Figs. 91, 158).

The palatal portions of the maxillary send a sharply pointed median process forward into the posterior part of the enormous incisive foramina. This and the equally pointed anterior end of the palatines are situated dorsal to the level of the adjacent cheek teeth, and form the roof of a prominent groove that extends from the incisive foramina to the middle of M^1 (Fig. 14A), and ends at the posterior palatine foramina.

The frontals are suturally separated for most of their length as seems generally to be true of caviomorphs, franimorphs, and paramyids (Wood, 1962a: Figs. 13A, 31A, 35A, 41A, 48A, 57A). The same is true of Old World hystricognaths. In PU

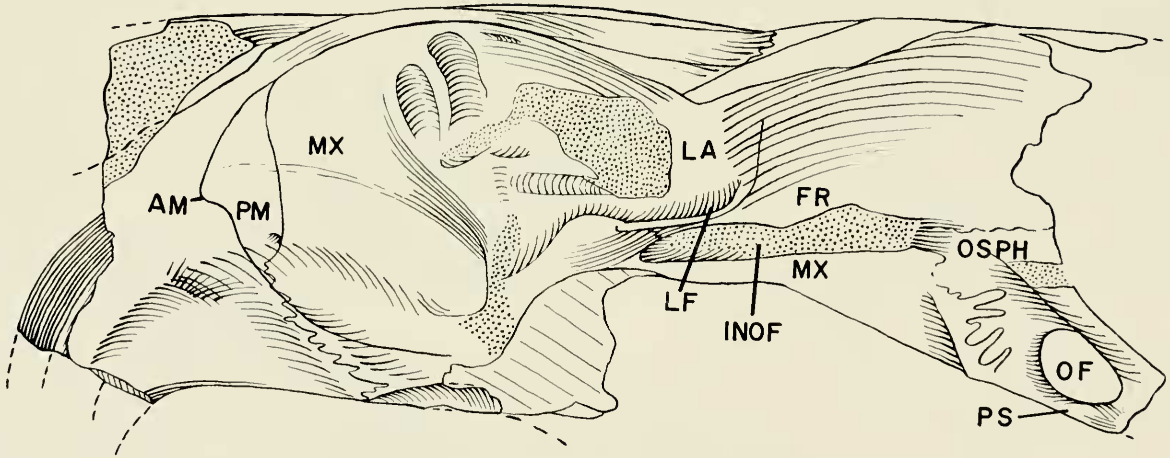

Figure 11. Partial skull of *Incamys bolivianus*, PU no. 20944, lateral view, ×4.

Abbreviations: AM—anterior limit of masseteric fossa; FR—frontal; INOF—interorbital fenestra; LA—lacrimal; LF—lacrimal foramen; MX—maxillary; OF—optic foramen; OSPH—orbitosphenoid; PM—premaxillary; PS—presphenoid. Dotted areas are matrix.

no. 21945 (Fig. 8A), the suture extends the entire length of the bones, as in *Myoprocta* and *Dasyprocta*. The dorsal surface is extremely flat, with slight longitudinal depressions on either side of the midline (Fig. 8A), as in *Neoreomys*. As noted above, the frontals narrow at the middle of the orbits. Within the orbit, the frontal is well preserved only in PU no. 21945 (Figs. 12, 15A). It was nearly as concave as in living dasyproctids. The orbital process of the frontal is essentially rectangular (Fig. 15A). The vertical lacrimo-frontal suture is hidden in Figure 12 by the lateral wall of the infraorbital foramen. At the posterior end, the frontal-squamosal suture is highly crenulate, but is also nearly vertical. Ventrally, the posterior three-fifths of the frontal meets the orbitosphenoid in a line that is generally straight but irregular in detail (Fig. 15A). The anterior part of the ventral border of the frontal is formed by the interorbital fenestra.

There is a small but pointed postorbital process of the frontal, somewhat behind the middle of the orbit (Figs. 8, 12), that extends out over the fossa for *M. temporalis*, as in *Dasyprocta* and *Myoprocta*. Behind this, and in the squamosal immediately behind the frontal-squamosal suture, is a smaller, rounded postorbital process. Between these two processes, an anterior slip of *M. temporalis* apparently extended a short distance onto the dorsum of the skull, arising entirely from the frontal (Fig. 8). There is no trace of the posterior postorbital process, or of any division of *M. temporalis*, in the skulls of *Neoreomys*, *Dasyprocta*, or *Myoprocta*. A similar condition, however, may be seen in the skull of *Myocastor* (Ellerman, 1940: Fig. 20). *M. temporalis* in caviomorphs is divisible into three portions which may be called the main, orbital and posterior parts (Woods, 1972: 129–130). The main part arises from the temporal fossa on the dorsum of the skull; the orbital from the frontal and squamosal within the orbit; and the posterior from the squamosal root of the zygoma (*op. cit.*). It would seem, therefore, that the orbital portion of *M. temporalis* must have been unusually large and distinct in *Incamys*, as would also seem to be the case in *Echimys* (Tullberg, 1899: Pl. 8, Figs. 7–8) and in *Proechimys* (Woods, 1972: Fig. 2A,B). It is possible that this is a primitive condition for caviomorphs. In the franimorphs, no skulls are preserved so as to show whether or not the orbital part of *M. temporalis* was visibly distinct on the dorsal surface. However, in *Paramys* (Wood, 1962a: 17; Figs. 2A,B; 13A,B), *Thisbemys* (*op. cit.*: Fig. 36A), and manitshines (*Pseudotomus*, *op. cit.*: 174; *Ischyrotomus*, *op. cit.*: 190; Figs. 68A,C; 71B,C; *Manitsha*, *op. cit.*: 222), the conditions are basically similar to those in *Incamys* except that, in this last genus, the fossa for the orbital part of *M. temporalis* is in the frontal; in the paramyids, it is in the alisphenoid or parietal. Among the thryonomyoids, there is possibly a rather similar situation in *Paraphiomys stromeri* (Lavocat, 1973: Pl. 2, Figs. 3–4; the specimen was not prepared enough for us to feel at all certain), and *Diamantomys luederitzi* (Lavocat, 1973: Pl. 3, Figs. 1–2), but rather clearly not in *Paraphiomys pigotti* (*op. cit.*: Pl. 1, Figs. 3–4) and apparently not in *Thryonomys* or *Petromus*.

The right lacrimal is partly preserved in PU nos. 20944 (Fig. 11) and 21945 (Fig. 12). There was a small expanse of the bone on the dorsum of the skull (Fig. 8) and it forms the posterior part of the dorsal root of the zygoma as in living dasyproctids and in *Neoreomys*. It is uncertain, due to breakage, just how far down the zygoma the bone extended. It may have reached the malar, as it does in *Neoreomys*. The opening of the nasolacrimal canal is near the posteroventral border of the bone. The canal curved forward and slightly ventrad. In *Neoreomys*, the opening of the canal is farther forward, on the lateral buttress of the lacrimal. In the living Dasyproctidae, the canal leads

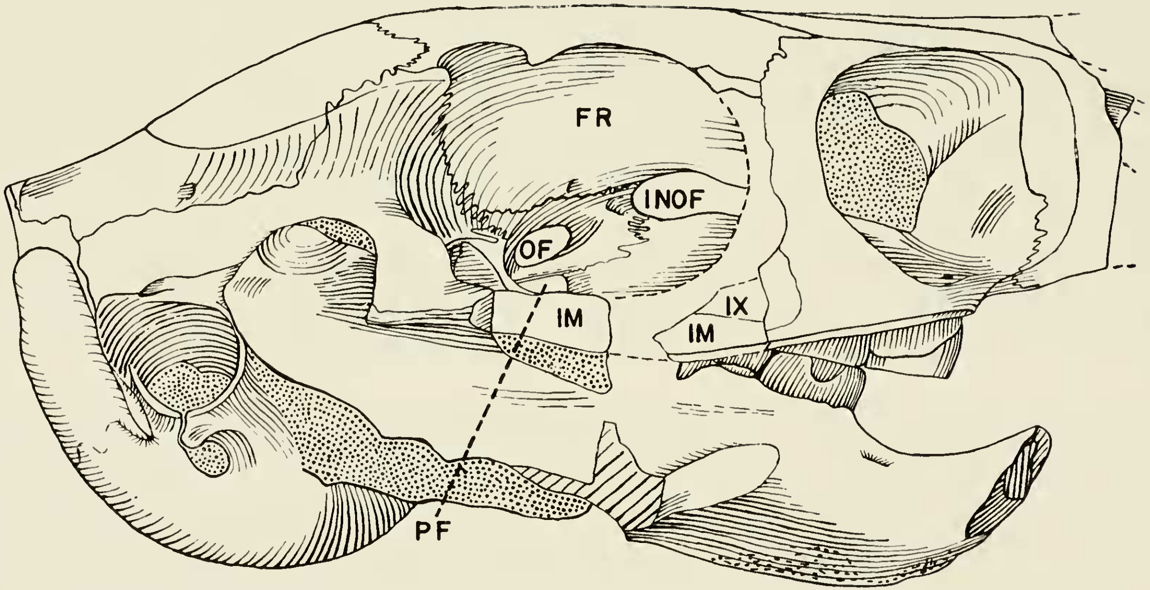

Figure 12. *Incamys bolivianus*, PU no. 21945, right lateral view of skull, ×3. Partly restored from left side.

Abbreviations: FR—frontal; IM—imprint of medial face of malar; INOF—interorbital fenestra; IX—imprint of medial face of maxillary; OF—optic foramen; PF—pterygoid fenestra.

forward and downward from the lacrimal foramen to the nasal passage, in a normal manner. However, half of its length is exposed by a large, oval opening in the medial wall of the masseteric fossa. There is a large opening in this position in *Neoreomys* (Scott, 1905: Pl. 64, Fig. 6), but not, apparently, in *Cephalomys* (Wood and Patterson, 1959: Fig. 21C). As preserved in *Incamys*, the course of the canal is a deep groove extending from the lacrimal foramen nearly as far as the rear of the upper incisor. Presumably, as also indicated by Lavocat (1976: 52), there was a thin lateral wall covering most of this groove, although there may have been an opening in it just behind the incisor. However, the preservation is such that we could not be certain whether or not the lateral wall was originally present in *Incamys*, or how large the supposed lateral opening might have been. The anterior limits of the lacrimal could not be determined because all specimens were broken in this area, but we find it impossible to visualize any construction of the lacrimal that would not have included a laterally directed buttress near its anterior end, supporting the dorsal root of the zygoma, a structure that is very characteristic of fossil and Recent dasyproctids, and that is also present in caviids and *Hydrochoerus*.

Small portions of both ends of the malar and the imprint of the medial surface of most of the remainder are preserved in PU no. 21945 (Fig. 12; IM). The ventral surface of the arch is uniformly rounded, as in *Myoprocta* and *Dasyprocta*. There is no suggestion of the pronounced ventral angulation seen in *Paraphiomys* (Lavocat, 1973: Pl. 1, Fig. 4). The anterior end of the bone is very similar to that of *Myoprocta*—much more so than like *Dasyprocta*. The malar forms a thin plate that lies on the lateral surface of the maxilla, which is exposed on the lateral side ventral to this thin plate. The imprint of the medial face of the zygoma shows the malar-maxillary contact rising posterodorsally across the arch. The preserved anterior portion of the malar is restricted to the horizontal bar of the zygoma, and does not extend far up the plate lateral to the infraorbital foramen, in this resembling both *Myoprocta* and *Dasyprocta*. How high it extended on the arch and whether or not it reached the lacrimal are undeterminable. The anterior malar-maxillary suture is slightly irregular, but not crenulate, and forms almost a straight line. The slender posterior tip of the malar extends a short distance behind the posterior end of the zygomatic process of the squamosal, as in *Myoprocta* and *Dasyprocta*. It is, however, more exposed in lateral view (Fig. 12) than in those genera.

The central part of the malar is missing. The imprint in the matrix preserves almost the entire ventral limit of the arch, and seems to preserve at least half of the dorsal limit. It is possible that part of the dorsal imprint has been broken away, although there is no evidence that it has. If the imprint of the central part of the malar is as complete as it seems to be, the bone was of essentially uniform dorsoventral diameter for its entire length, resembling *Myoprocta* and *Dasyprocta* in this, but perhaps being a little less enlarged anteriorly. There is absolutely no similarity in any respect to the malar of *Paraphiomys* (Lavocat, 1973: Pl. 1, Fig. 4; Pl. 2, Fig. 4) or *Diamantomys* (*op. cit.*: Pl. 3, Fig. 2), both of which form heavy vertical plates.

The fused palatines extend forward to the middle of P^4 or dm^4, as in *Dasyprocta*. Lavocat (1976: 52) stated that the maxillary-palatine suture reaches the level of the posterior end of P^4. A careful examination of his stereophoto (*op. cit.*: Pl. 3, Fig. 1) suggests that, if this area had been completely prepared, the suture would probably have the position shown in our Fig. 14A. The maxillary-palatine sutures diverge posteriorly, at first abruptly, then very gently, and then abruptly again behind M^3. The posterior palatine foramina are completely enclosed by the palatines. On the midline, the palate ends opposite the middle of M^2 (Fig. 14A) as in *Cephalomys*. Lavocat (1976: 54) suggests that there may have been a rudimentary median process at the midline of the posterior margin of the palate of the type (1976: Pl. 3, Fig. 2); one clearly was absent in PU no. 21945 and in the slightly younger PU no. 21726 (Fig. 14A). The palatine forms the lateral walls of the pharyngeal passage behind the rear of the hard palate, reaching almost to the front of the pterygoid fossa (Fig. 15B), about as in *Reithroparamys* (Wood, 1962a: Fig. 41B), the only franimorph in which any of this area is known. The palatine-pterygoid suture is highly crenulate. In both of these respects, *Incamys* is very similar to *Dasyprocta* and *Myoprocta*.

In PU no. 21945, the palatine-pterygoid suture very clearly lies behind the middle of the "orifice choano-orbitaire" (choano-orbital fenestra), as stated by Lavocat, and as shown in Fig. 15B, but there is what might be another suture along the lateral wall of the pharyngeal passage anterior to this (Fig. 15B; ?). It is very doubtful that this really is a suture; irregularities in this area that are vaguely suture-like can be seen in some individuals of *Dasyprocta*. The orbital process of the palatine extends along the front of the choano-orbital fenestra up to the orbitosphenoid (Fig. 15A). We do not know whether this fenestra has any great significance or not. A similar opening is present in many sciurids, but absent in others, varying from present to absent within the genus *Sciurus*.

The orbitosphenoid is a large bone. Its dorsal margin is somewhat higher than the dorsal limit of the alisphenoid, and it separates that bone from the frontal (Fig. 15A). The suture between the orbitosphenoid and the maxillary is irregular, especially in its anterior portion, just beneath the rear of the interorbital fenestra (Fig. 15A). After a short, generally vertical contact, the suture turns backward nearly horizontally, the anterior portion of the orbitosphenoid lying dorsal to the maxillary. Below the posterior portion of the bone is the orbital opening of the choano-orbital fenestra (Fig. 15A), that opens both into the pharyngeal passage between the pterygoid and the presphenoid, and also into the pterygoid fossa. The confluent optic foramina are entirely within the orbitosphenoid. The bone forms the median wall of the foramen lacerum anterius (Fig. 15A).

The pterygoid forms the anterior end of the pterygoid fossa and its median wall (Fig. 15B). The internal pterygoid process, preserved *in toto* only on the right side of PU no. 21945, is a long, slender process, reaching back to touch the anteromesial tip of the bulla (Fig. 15B), as in the living dasyproctids. It is bounded dorsally by the usual vacuity between it and the bulla.

The alisphenoid, as in other post-Eocene hystricognaths, is reduced in height, extending, in the temporal fossa, little if any above the level of the glenoid cavity (Figs. 12, 15A). It is separated from the frontal by a narrow strip of the orbitosphenoid, a significant difference from the African *Paraphiomys* (Lavocat, 1973: 31). Anteriorly, the alisphenoid forms the lateral wall of the foramen lacerum anterius. The dorsal border of the bone runs back in essentially a straight line, below the zygoma, to the front of the bulla. Ventrally, the alisphenoid forms the lateral wall of the pterygoid fossa, reaching the palatine just in front of the point where the pterygoid fossa begins (Fig. 15A). There is a broad shelf of the alisphenoid, behind the pterygoid fossa, separating the fossa from the large foramen lacerum medium (Fig. 15B). This seems to be homologous to the shelf in *Paraphiomys* (Lavocat, 1973: Pl. 2, Fig. 2) but differs in that, in the African form, it is at the level of the dorsal portion of the pterygoid fossa, whereas, in *Incamys* (Fig. 15B), it is ventral to the fossa. The fossa and the foramen lacerum medium join dorsal to this shelf.

The pterygoid fossa is short, wide, very deep, and perforate (Fig. 15B). It is much wider than in *Neoreomys* or the living dasyproctids. We have been unable to determine what, if any, dorsal border there may have been to the pterygoid fossa, the alisphenoid wall being very thin, so that it is easy to cause damage inadvertently. Nor have we been able to detect any indication, within the dorsal fenestra, of a partition between the alisphenoid canal and the passage for *M. pterygoideus internus*. However, in view of the damage sustained by the specimen prior to burial and of the delicate nature of the bony separation in various hystricognaths, little significance can be attached to this. We believe that the openings in this region described here were all that were present in life; however, the thinness of the bone and the pre-fossilization damage that had occurred to the presphenoid, basisphenoid and basioccipital of PU no. 21945 (Fig. 15B) shows how much serious disintegration can occur, even in heavy bones on an otherwise well preserved skull. Lavocat's material of *Incamys* apparently did not preserve this area.

Along the medial wall of the fossa, there is a large opening, separating the internal pterygoid process from the presphenoid (Fig. 15B). This is the palatal opening of the choano-orbital fenestra discussed above. The function of this opening is not known to us. Comparable openings occur in some other hystricognaths, among them *Neoreomys* and the living dasyproctids. A thin bar of the presphenoid separates this fenestra from another one posteromedial to it, that lies mainly within the basisphenoid, although extending for a short distance into the presphenoid. We apply the noncommittal term sphenoidal fenestra to it, and confess total ignorance as regards its function (Fig. 15B; SF). We do not know of any other rodents in which this fenestra occurs.

The parietals have undergone crushing and buckling in most specimens, but are perfectly preserved in PU no. 21945 (Fig. 8A). They are, as shown by the dorsal contour of the occiput (Fig. 10B), much less arched transversely than those of *Neoreomys* and the living dasyproctids. In PU no. 21945 there seems to be a short section of suture still visible between the parietals (Fig. 8A); in other specimens, there is no trace of such a suture. The parietals resemble those of the Recent dasyproctids in general outline (Fig. 7), but the anterolateral corners extend forward (Fig. 8A), more as in *Neoreomys*. Faint, lyrate crests converging at the sagittal crest mark the medial limits of the weakly-developed temporal fossae. The sagittal crest is small and weak, as in *Myoprocta*. In contrast to *Platypittamys*, but in agreement with the great majority of caviomorphs (p. 488), there is no trace of a separate interparietal. Near the lateral margin of the parietal, directly above the porus acusticus externus, a fair-sized vascular foramen leads forward into the bone (Fig. 8A). The parietal extends, for the middle half of the width of the occiput, back almost to the top of the lambdoid crests. Laterally, however, the posterior margin of the parietal is bowed forward (perhaps indicating the lateral limits of the otherwise unidentifiable interparietal) by the lateral process of the occipital.

The squamosal is fundamentally similar to that of other members of the family. Posteriorly it is excluded from the occipital crest by the exoccipital. It is tightly appressed to the dorsal portion of the tympanic, but, in contrast to other dasyproctids, does not extend posteriorly beyond the porus. A small subsquamosal foramen is situated directly above the porus acusticus externus (Fig. 12); on the left side of PU no. 21945 this foramen is partially divided into anterior and posterior portions. Anterodorsally, the squamosal extends to, and largely forms, the posterior postorbital process (Figs. 8, 12). The frontosquamosal suture bends backward, below the posterior postorbital process, and then runs almost vertically down behind the frontal to the level of the glenoid cavity. Below here, the frontosquamosal suture becomes highly crenulate, in contrast to the essentially smooth suture in modern dasyproctids and the slightly crenulate one in *Neoreomys*. Finally, this portion of the squamosal makes contact, ventrally, with the alisphenoid, slightly below the level of the glenoid (Fig. 15A). From here, the alisphenoid suture runs almost directly backward, below and medial to the glenoid cavity, until it reaches the front of the bulla. It is uncertain how far forward the squamosal extended on the zygoma; certainly no farther than the middle of the arch (Fig. 8).

The bulla is not preserved in the type; it is apparently partially preserved but still buried in the matrix in the type of *I. pretiosus* (Lavocat, 1976: 58), although we have been unable to recognize any trace of it in Lavocat's stereophotos (1976: Pl. 5, Figs. 6–7; Pl. 6, Figs. 4–5). In the skulls of PU nos. 21726 and 21945 (Figs. 10A, 12, 14), it is firmly attached and very large, about one quarter the length of the skull. It is roughly comparable in size to those of *Platypittamys*, *Chinchilla*, *Schistomys*, *Microcavia* and other small caviomorphs, and is relatively larger in all dimensions than those of other dasyproctids. Size apart, however, there is a similarity in shape and other features to the dasyproctid bulla. Widest and deepest anteriorly, the bulla of *Incamys* extends from a point in advance of the basioccipital-basisphenoid suture to the back of the condyle. The ventral surface is strongly arched, both anteroposteriorly and transversely. The anterior face is very gently convex. The anterior part of the medial surface is parallel to the long axis of the skull; the posterior part is inclined posterolaterally around the condyle (Fig. 15B). The basisphenoid and basioccipital press tightly against the anterior half of the bulla. In the posterior portion, where the bullae diverge, there is a narrow trench between the bulla and the basioccipital. The posterior portion of the trench is occupied by the foramen lacerum posterior (Fig. 15B). Partially separated from the anterior end of this is what seems to be another opening, leading forward. If this actually is a foramen, it may be a vestigial carotid canal, or it may have transmitted a vein. We incline to the latter alternative since some individuals of *Dasyprocta* have a similarly situated small opening, and Bugge (1974a: 54) found no trace of an internal carotid in that form. No other specimen of Deseadan caviomorph is sufficiently well preserved (and prepared) to demonstrate the presence or absence of this opening (see pp. 484–486 for a discussion of the carotid circulation in hystricognaths).

The porus acusticus externus is large and extends posterodorsally, imparting an oval outline to the opening (Fig. 13). Posteriorly, its rim forms a narrow ridge bounded behind by a deep and narrow groove. The tympanohyal articulation and the adjacent stylomastoid foramen are situated at the ventral extremity of the groove. The anteroventral lip of the porus acusticus is prominent and elevated on PU no. 21945, as in *Neoreomys*. There is a notch at the middle of the ventral wall of the porus, from which a deep, initially narrow, curving slit extends downward, then enlarging (Fig. 13), as in *Neoreomys* and young individuals of *Dasyprocta*, giving a figure eight shape to the opening. The anterior lip of the porus is somewhat thickened, but not so much so as in *Neoreomys*, and is perforated by a minute foramen. The porus is completely surrounded by the tympanic, as in rodents generally. Following Van Kampen (1905: Fig. 59), there has been some ten-

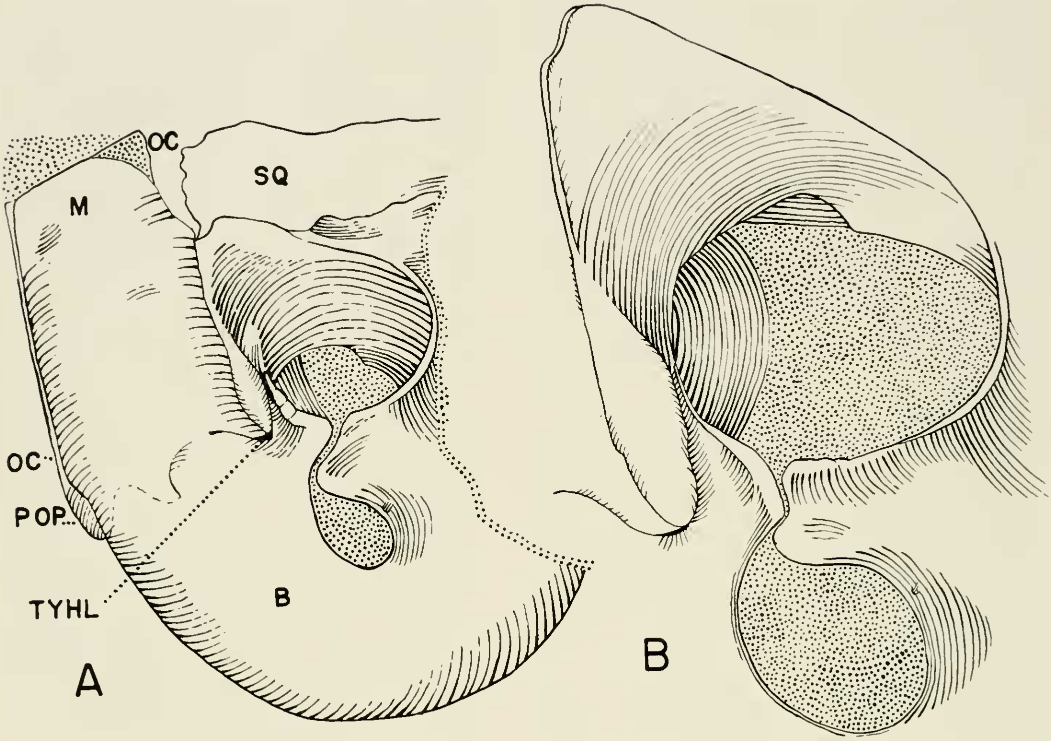

Figure 13. *Incamys bolivianus*, PU no. 21945, parts of right ear. A. Lateral view of bulla from somewhat behind and below, ×5. B. Lateral view of porus acusticus externus, ×10.

Abbreviations: B—bulla; M—mastoid process; OC—occipital; POP—paroccipital process; SQ—squamosal; TYHL—area of articulation of tympanohyal.

dency (e.g., Grassé and Dekeyser, 1955: 1334) to regard the portion of the bulla above the porus as being composed of the periotic. Evidence of its tympanic nature in rodents is, we believe, provided by certain paramyids, especially *Ischyrotomus oweni* (Wood, 1962a: 207), in which the bulla, found detached from the periotic, completely surrounds the opening of the porus. That part of the bulla dorsal to the porus is not so large as in other dasyproctids, especially posteriorly. A prominent groove runs backward from the anterior border nearly to the center of the anterior margin of the porus (Fig. 10); comparable, although shallower and more dorsally placed, grooves are present in *Neoreomys* and modern dasyproctids.

Posteriorly, the bulla narrows, as in other dasyproctids, and just reaches the short paroccipital process. Breakage in the right bulla of PU no. 21726 (Fig. 14A) reveals the lower part of the crista tympanica. The groove lateral to it is larger and deeper than in *Dasyprocta*, and is partially divided by at least three cross struts, features not present in the living forms. Within the matrix-filled tympanic cavity of PU no. 21726 are small pieces of bone; unfortunately, the extreme hardness of the rock has prevented further preparation, and it is impossible to determine whether these are exposed portions of the auditory ossicles or fragments of the bullar floor.

The mastoid process is large and in-

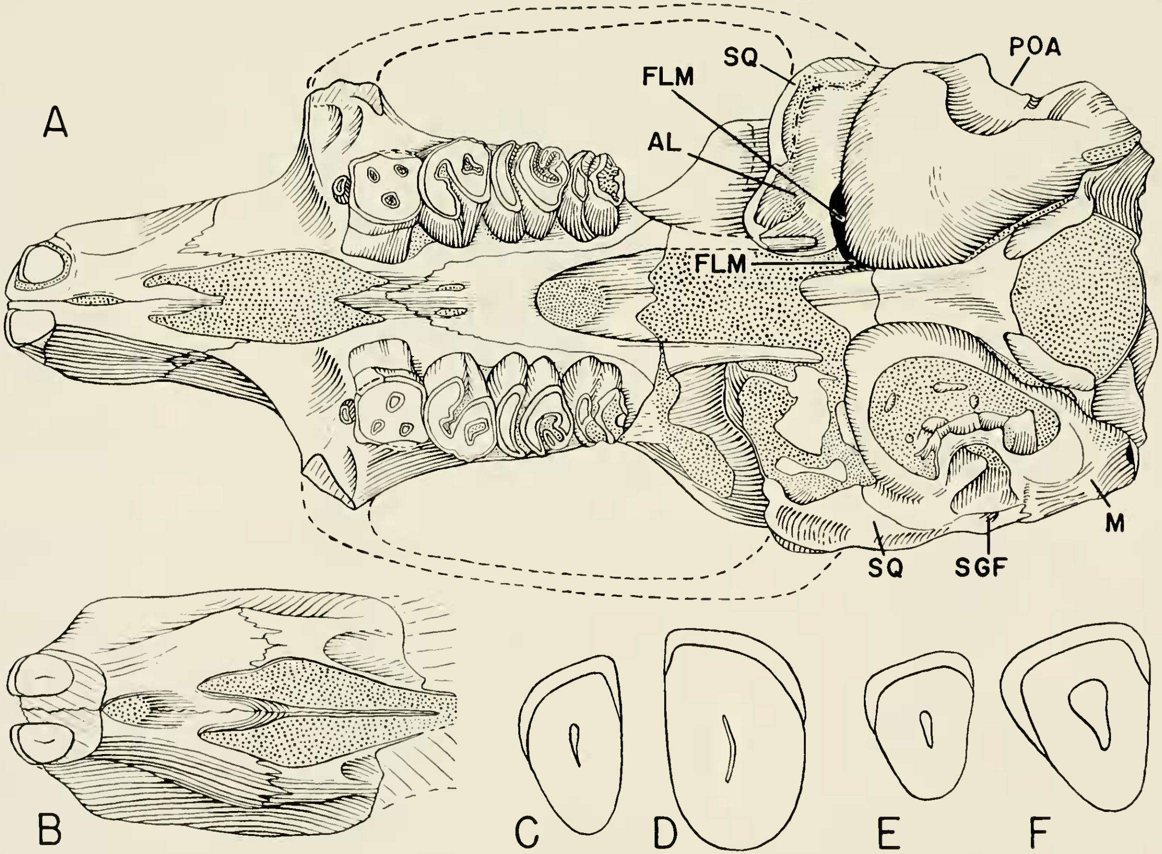

Figure 14. Skulls of *Incamys bolivianus*, ventral view, and incisors. A–B, ×3; C–F, ×10. Dotted areas are matrix. A. PU no. 21726, juvenile. B. PU no. 20944, partial skull. C. PU no. 21726, cross section of LI^1 from front. D. PU no. 20944, cross section of LI^1 from front. E. PU no. 21726, cross section of LI_1 from front. F. PU no. 21735, cross section of LI_1 below diastema.

Abbreviations: AL—alisphenoid; FLM—foramen lacerum medium; M—mastoid; POA—porus acusticus externus; SGF—supraglenoid foramen; SQ—squamosal.

flated, participating to a greater extent in the lateral surface of the skull than in other dasyproctids, and is visible in posterior view (Fig. 10B). Due to the inflation it merges smoothly with the posteroexternal surface of the bulla. A thin strip of the exoccipital, narrower than in other members of the family, separates it from the squamosal. Breakage on the left side of PU no. 21945 reveals that the inflated sinus of the mastoid was crossed by a number of septa. What may be the suture between the tympanic and the mastoid is shown in Fig. 13A, but we are not certain either that it is the suture or that we have located it correctly in its entirety.

The ventral part of the skull between the palate and the bullae is not preserved in the type (Lavocat, 1976: Pl. 3, Fig. 2), and in Lavocat's type of *I. pretiosus* only the endocranial surface has been prepared, which, as Lavocat stated (1976: 56), makes comparisons difficult. This area is badly broken in PU no. 21726, but part of it is very well preserved in PU no. 21945 (Fig. 15B). Even in this specimen, however, the ventral surfaces of the presphenoid, basisphenoid and basioccipital were damaged, before fossilization.

The presphenoid is a long, slender bone, its posterior end being just behind the anterior limit of the pterygoid fossa. Its posterior portion forms the median wall of the pterygoid fenestra. There is a lateral brace, near the posterior end of the bone, running posterolaterally to the alisphenoid and pterygoid, and forming the anterior border of the sphenoidal fenestra. The presphenoid is more slender, relatively, than in *Neoreomys*, and more comparable to that of *Myoprocta*.

Enough of the basisphenoid is preserved to reveal that there was an angle between it and the basioccipital on the ventral surface, comparable to that in other dasyproctids. Otherwise, it is badly damaged in all available specimens. Its anterior extremity surrounds most of the sphenoidal fenestra.

The basioccipital is widest at the condyles, narrows rapidly forward for half its length, and then maintains an even width for the remainder of its course. The ventral surface of the basioccipital in PU no. 21945 bears a strong median keel; its height is largely due to the crushing of the adjoining bone (Fig. 15B). The trench between the lateral margin of the basioccipital and the bulla has been described above. The foramen lacerum medium lies in front of the bulla at its junction with the basioccipital and basisphenoid.

The occiput is essentially vertical, as in *Neoreomys*. The supraoccipital is less arched than in that form or in the Recent dasyproctids, and extends over onto the dorsal surface only for a very short distance at the center (Figs. 7, 8A), in contrast to other dasyproctids but in agreement with *Platypittamys*; on the sides, however, it plays a larger part in the formation of the roof, agreeing in this with other dasyproctids and differing from *Platypittamys*. The lateral portion, separating the mastoid from the squamosal (Figs. 7, 8, 12; p. 487) starts out, at its mesial end, as a slender process between the central part of the parietal and the dorsal tip of the mastoid. It then widens considerably, separating the mastoid from the squamosal and lateral part of the parietal (Fig. 8A). At about mid-height of the squamosal, however, the process abruptly narrows (Figs. 10, 12, 13A) and extends as a very slender sliver of bone to just below the ventral limit of the squamosal, at the posterodorsal limit of the tympanic.

The suture between the exoccipital and the mastoid follows a ridge that runs laterally and a little dorsally from the upper part of the foramen magnum, as it does in other members of the family. Dorsal and ventral to this ridge are depressions for attachment of neck muscles (the depth of the dorsal one is exaggerated in PU no. 21726, Fig. 10B, due to breakage). There is an indication of a vertical crest running from the top of the foramen magnum to the occipital crest.

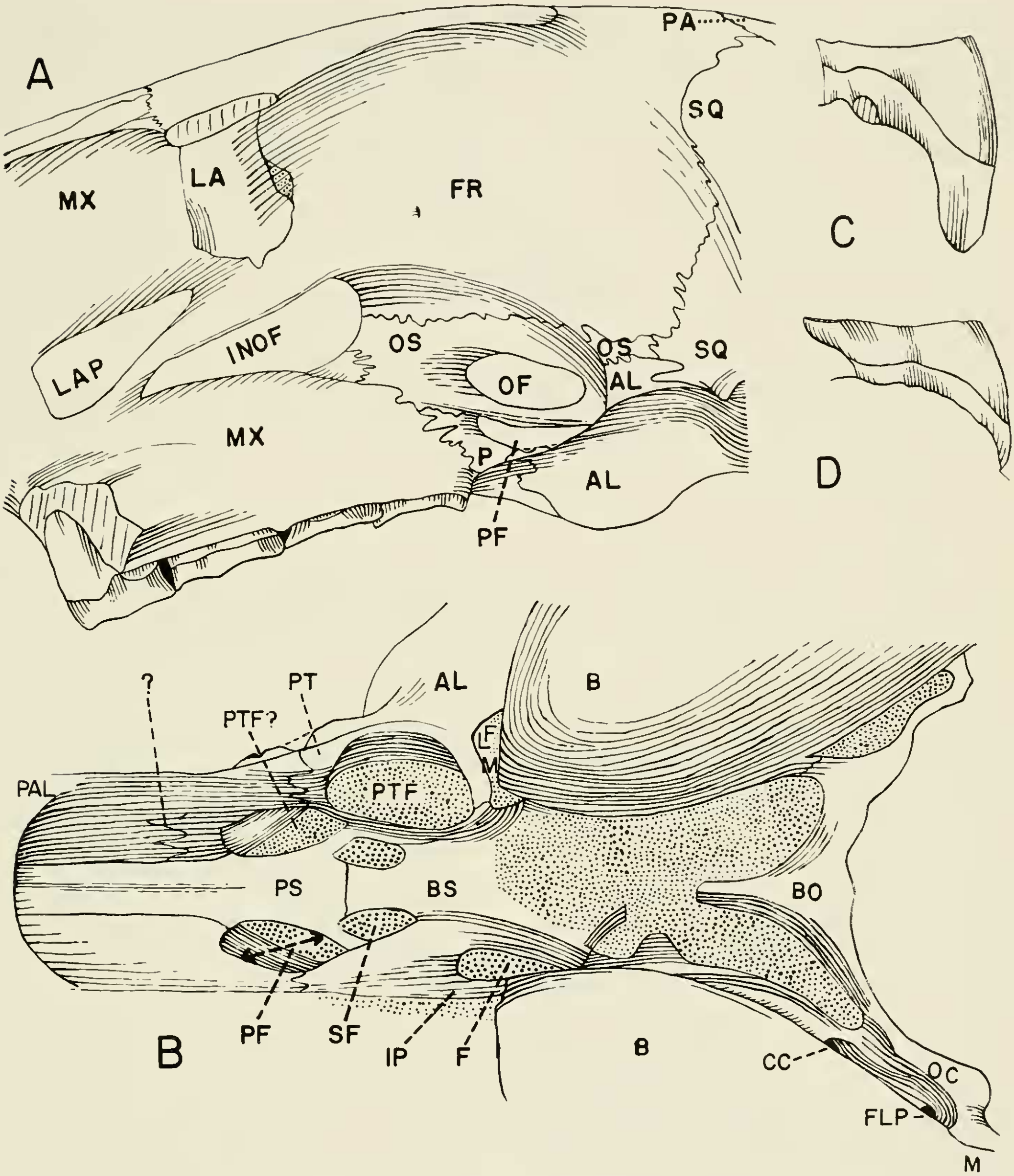

Figure 15. *Incamys bolivianus*, ×5. A–B. PU no. 21945, anterior end to the left. A. Oblique view of left orbit and temporal fossa. B. Ventral surface of basicranium. C–D. Posterior views of right upper molars, showing change in width of occlusal surface with wear. C. PU no. 20950, slightly worn M^1 or M^2. D. PU no. 20955, highly worn M^2.

Abbreviations: AL—alisphenoid; B—bulla; BO—basioccipital; BS—basisphenoid; CC—possible carotid canal; F—vacuity between internal pterygoid process and bulla; FLM—foramen lacerum medium; FLP—foramen lacerum posterior; FR—frontal; INOF—interorbital fenestra; IP—internal pterygoid process; LA—lacrimal; LAP—opening in wall of lacrimal canal; M—mastoid; MX—maxillary; OC—occipital; OF—optic foramen; OS—orbitosphenoid; P, PAL—palatine; PA—parietal; PF—choano-orbital orifice; PS—presphenoid; PT—pterygoid; PTF—pterygoid fossa; PTF?—possible extension of pterygoid fossa; SF—sphenoidal fenestra; SQ—squamosal; ?—probably a pseudosuture.

The paroccipital process is short, squat, and attached to the posterior surface of the mastoid and bulla, somewhat as in the octodontid *Sciamys* (Scott, 1905: Pl. 67, Fig. 9); in other dasyproctids it is longer and freely projecting.

The condyles are narrow, face ventrally as much as posteriorly—as in Recent dasyproctids—and lie closely alongside the bullae for much of their lengths. Inflation of the auditory region has brought much more of the lateral surface of the cranium into view from the occipital aspect than is the case in other members of the family. The foramen magnum is essentially circular and very large.

The mandibular fragments at our disposal (Figs. 12, 16) show that the horizontal ramus was approximately as deep and wide as that of *Cephalomys*. The posterior part of the dorsal border of the diastemal surface sloped gently downward and forward at almost the same angle as in that form and in *Neoreomys*, not so abruptly nor so deeply as in the living dasyproctids. The masseteric crest begins beneath the center of P_4 and agrees in size with those of other members of the family (Fig. 16A,B). The low coronoid (Fig. 16B) passes the alveolar level a little behind M_3, as in *Cephalomys*, and in contrast to the more forward position in later forms. The coronoid is clearly too large in Lavocat's reconstruction (1976: Fig. 31). The condyle is an elongate oval, presenting dorsally, compressed laterally, and nearly on a level with the cheek teeth (Fig. 12); the postcondyloid process is moderately developed. The mental foramen is high and a little in front of P_4. It opens upward (Fig. 16B). A peculiar feature is the remarkable number of minute vascular foramina along the course of the incisors (Fig. 16D); none of Lavocat's figures show this area. Similar foramina, although not in such rich profusion, also occur in the living dasyproctids. As in the living forms, the posteroventral portion of the symphysis extends back beneath P_4. The genioglossal pit is very weakly developed.

Cement is lacking on all cheek teeth. The teeth are larger relative to skull size than in the living dasyproctids, being closer to *Neoreomys* in this respect. For terminology of the parts of the cheek teeth, see Figs. 1–2 (pp. 376–377). The upper teeth are inclined posteriorly, the lowers anteriorly. In both uppers and lowers the major lophs and lophids unite with wear into an S-shaped pattern, the S running from the lingual end of the anteroloph to the labial end of the posteroloph in the uppers and from the metaconid to the hypoconid in the lowers. This is especially evident after an intermediate amount of wear (Figs. 18A, 19G). The enamel over unworn crowns is thinner than that on the sides, as is shown by its thinness around the edges of lophs and lophids of slightly worn teeth.

The cheek teeth display unilateral hypsodonty, especially notable in the uppers which are hypsodont lingually and brachyodont labially (Fig. 17E). The mesodont lower teeth show much less disparity in height of crown, although the enamel descends lower on the labial and posterior faces (especially on the hypoconid) than on the lingual and anterior ones. This pattern for the initial stages in the development of hypsodonty is exceedingly common among the Rodentia, and cannot be taken to indicate any special relationships of *Incamys* with any other genus or group of genera.

The unilateral hypsodonty of the upper teeth results from the fact that there is no post-eruptional growth of the labial margin of the crown, whereas there is long continued growth of the lingual half of the tooth. As a result, eruption causes a tooth to rotate, in a transverse plane, about the buccal roots. The center of rotation is approximately at the point where the roots clear the alveoli. From this it ensues that there is extensive wear on the lingual half of the crown, and little wear on the extreme labial parts, which gradually extend farther and farther labially as rotation progresses. This is demonstrated by the posterior views of two up-

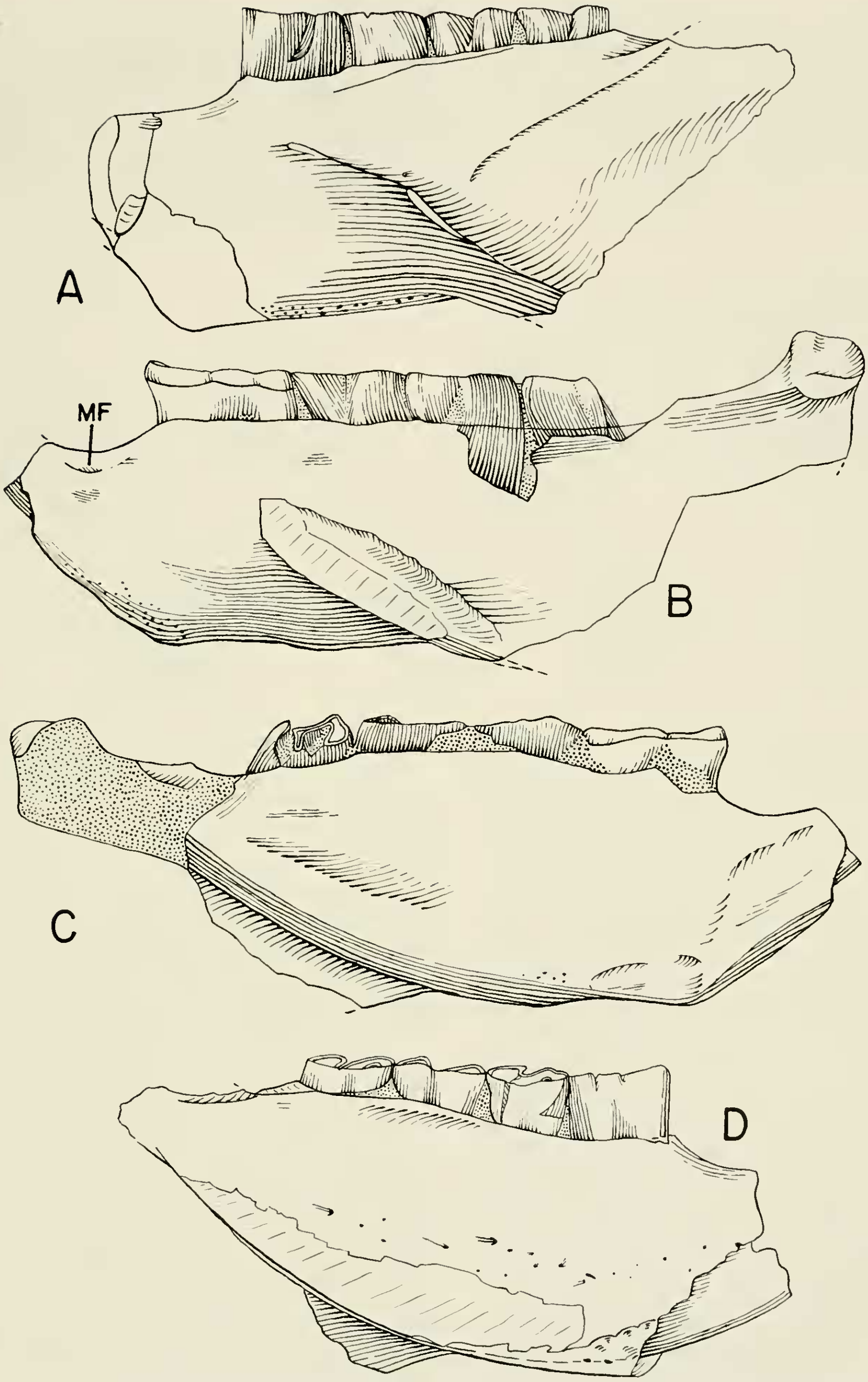

Figure 16. Lower jaws of *Incamys bolivianus*, ×4. Dotted areas are matrix. A. Lateral view of PU no. 20933, completed from PU nos. 20921, 20925, and 20941. B. Lateral view, PU no. 21726. C. Mesial view, PU no. 21726. D. Mesial view, PU no. 20933.

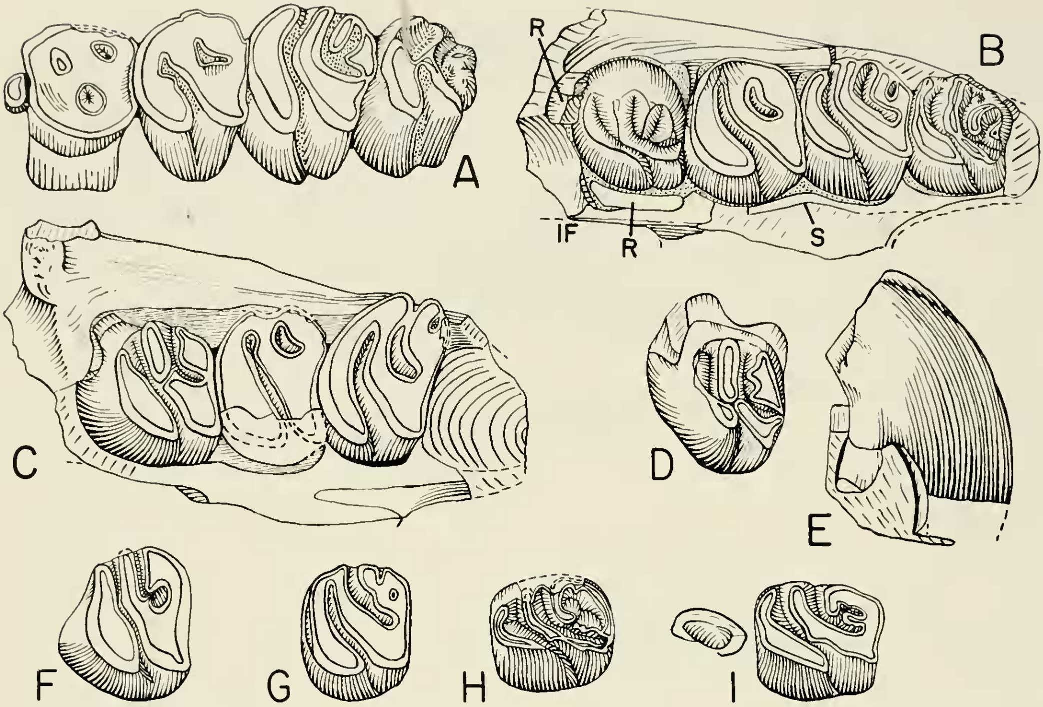

Figure 17. Left upper cheek teeth of *Incamys bolivianus*, anterior ends to the left, ×5. Dotted areas are matrix. A. PU no. 21726, dm^{3-4}, M^{1-3}. B. PU no. 21728, P^4–M^3. C. PU no. 20960, P^4–M^2. D–E. PU no. 20965, P^4. D. Occlusal view. E. Anterior view. F. PU no. 20963, P^4. G. PU no. 20968, $M^{1\ or\ 2}$. H. PU no. 20981, dm^4. I. PU no. 20980, dm^4 and root of dm^3.

Abbreviations: IF—incisive foramen; R—roots of dm^4; S—maxillary-palatine suture.

per molars. In the less worn tooth (Fig. 15C), the wear surface ends essentially ventrad of the labial margin of the buccal roots; in the worn tooth (Fig. 15D), the wear surface extends 1 mm or more beyond the labial margin of the roots. The situation just described is particularly characteristic of M^{1-2}. In both P^4 and M^3, the absence of adjacent teeth on one side has permitted the forward (or backward) growth of the hypsodont lingual portion, and the rotation of the tooth as eruption proceeds is not in a simple transverse plane. Therefore, these teeth do not increase so markedly in width with wear as do M^{1-2}, although an increase does occur (Table 3). The anteroposterior diameters of P^4–M^2 remain approximately constant as wear proceeds. That of M^3 increases in length with wear, but we have not computed σ and V for this tooth, as we did not have an adequate sample. Again, because of the size of the sample, we are not sure whether this tooth is or is not significantly smaller than the others (Table 3). P^4, however, does not differ greatly in size from the molars.

Lavocat (1976: 42) indicated that P^4 is smaller than M^{1-2}. This opinion is at least partly due to the fact that, of the three specimens he figured, two (the type, SAL 117, Lavocat, 1976: Pl. 4, Fig. 1 and SAL 118, Lavocat, 1976: Pl. 4, Fig. 2) have P^4 in process of eruption and the greatest diameters of these teeth are still intra-alveolar. The third specimen (SAL 163, Lavocat, 1976: Pl. 4, Fig. 4), which Lavocat referred to *I. pretiosus*, is an iso-

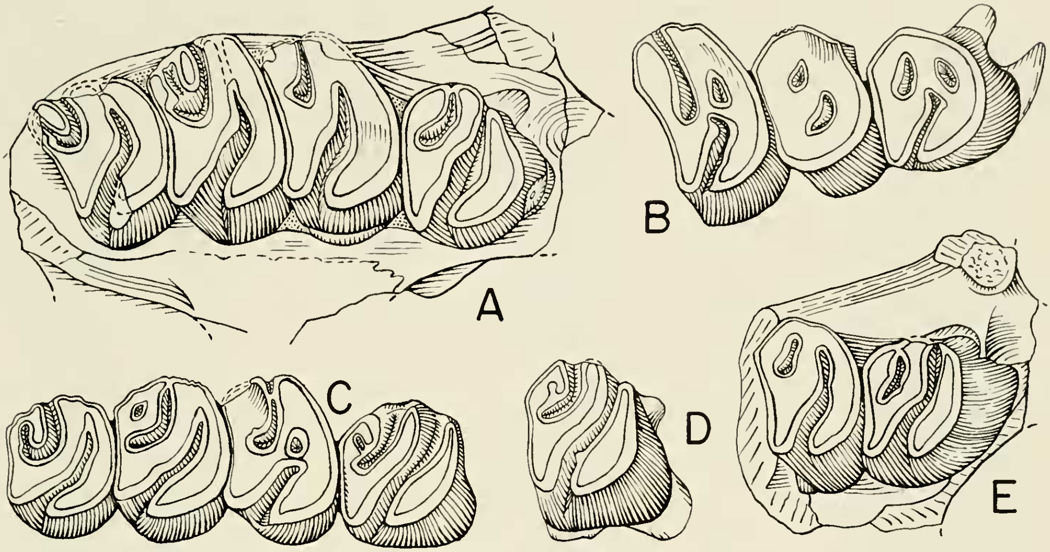

Figure 18. Right upper cheek teeth of *Incamys bolivianus*, anterior ends to the right, ×5. A. PU no. 20947, RP^4–M^3. Part of zygomatic root added from PU no. 20938; anterior part of maxillary-palatine suture from PU no. 20954. B. PU no. 20955, RP^4–M^2. C. PU no. 20943, RP^4–M^3. D. PU no. 20939, RP^4. E. PU no. 20956, RP^4–M^1.

lated P^4, and thus its size cannot be compared with that of M^1 or M^2.

In the lower teeth, P_4 is longer than the rest, and M_2 is the widest of the molars (Table 4). The most variable factor in the lower cheek teeth is the length of M_3. The length of the wear surface is to a great extent dependent on age, and is (otherwise) essentially meaningless. We have therefore taken the greatest extra-alveolar length of the crown as the anteroposterior diameter of the tooth. In cases where the entire alveolar border is preserved, we believe this measurement to be a homologous one. However, M_3 is implanted at an angle (Fig. 16B,C), so that the crown of the tooth extends a considerable distance behind the rear of the alveolus, within that cavity. A recheck of a number of specimens with unusually large anteroposterior diameters for M_3 showed that in most cases the unusually long measurements resulted from the fact that the posterior margins of the alveolus were damaged or destroyed.

Because of the element of uncertainty as to the length of M_3 and the variation of transverse diameters of M^{1-2} with age, we have prepared Tables 3–4 both to include all specimens as originally measured and to exclude the anteroposterior diameters of M_3 where the location of the posterior margin of the alveolus is uncertain and the transverse diameters of all specimens of M^{1-2} where the buccal margin of the crown extends 1 mm or more beyond the labial margin of the roots (Fig. 15D).

Lavocat (1976: 42–43) discussed the homologies of the various parts of the upper cheek teeth of *Incamys*. We are in agreement with him that the anterior crest is an anteroloph uniting lingually with the protocone, and that the second crest is the protoloph uniting lingually with the hypocone. On the labial sides of the crowns of unworn teeth there are two large, subequal cusps, continued lingually by ridges reaching about halfway across the teeth (Fig. 17A, M^{2-3}; 17B, P^4,

TABLE 3. MEASUREMENTS, IN MM, OF UPPER TEETH OF *Incamys bolivianus*.

	N	OR	$\bar{X}$	σ	V
P^4–M^3 or dm^3–M^3	7	11.2–14.0	12.70		
dm^3 anteroposterior	2	.61–.68	.65		
transverse	2	1.08–1.27	1.18		
dm^4 anteroposterior	5	2.83–3.47	3.14		
width protoloph	4	2.81–3.68	3.30		
width metaloph	2	2.95–3.47	3.21		
P^4 anteroposterior	21	3.04–4.11	3.59	±.29	8.05
width protoloph	21	3.28–4.50	3.77	±.27	7.16
width metaloph	20	3.25–4.36	3.85	±.36	9.35
M^1 anteroposterior	22	2.61–3.30	2.91	±.17	5.84
width protoloph*	16	3.40–5.8	4.15	±.56	13.49
width protoloph#	13	3.40–4.60	3.98	±.37	9.30
width metaloph*	13	3.32–5.8	4.03	±.73	18.11
width metaloph#	10	3.32–4.24	3.69	±.26	7.05
M^2 anteroposterior	14	2.68–3.48	3.00	±.22	7.33
width protoloph*	15	3.40–5.68	4.13	±.76	18.40
width protoloph#	12	3.40–4.29	3.80	±.31	8.16
width metaloph*	13	3.44–5.6	4.14	±.71	17.15
width metaloph#	10	3.44–4.51	3.80	±.32	8.42
M^3 anteroposterior	9	2.43–3.39	2.87		
width protoloph	8	2.84–4.54	3.61		
width metaloph	6	2.81–3.48	3.12		
I^1 anteroposterior	5	2.35–3.13	2.76		
transverse	6	1.40–2.13	1.72		
ratio	5	.60–.70	.64		

* Including all specimens.

Excluding PU nos. 20929, 20947, and 20955. The rationale for making computations omitting these specimens is discussed in the text.

M^{2-3}; Lavocat, 1976: Pl. 4, Fig. 1, P^4). At the rear of the teeth is a crest that we and Lavocat agree is the posteroloph.

The crux of our differences lies in the nature of the two labial cusps. We believe them to be the paracone and metacone (Fig. 1A–C; PA, ME), as they are subequal and occupy the normal mammalian positions for such cusps. Lavocat accepts the anterior as the paracone, but interprets the second as the labial end of the mesoloph, more specifically (1976: 45) as a mesostyle, which would therefore (although he does not say so) mimic the normal metacone. Lavocat (1976: 42) stated that the structures of this area in the thryonomyoids "sont morphologiquement absolument comparables." We cannot understand this statement, since the upper teeth of the most primitive known thryonomyoid, *Phiomys andrewsi* of the early Oligocene (Fig. 30C), have a paracone and metacone (recognized as such by him) fundamentally like what we consider to be the paracone and metacone in *Incamys*, but separated by one or more intermediate crests (two in Fig. 30C), at least one of which must be the mesoloph. A very similar pattern is present in the more advanced *Metaphiomys schaubi* (Fig. 30D), also from the early Oligocene. In *Incamys*, there certainly is no trace of a crest that could be a mesoloph between what we believe to be the paracone and metacone.

Lavocat pointed out that some thryonomyoids such as *Gaudeamus*, with a reduced number of crests, are found in association with the more primitive five-crested ones. He is entirely correct in this, and *Gaudeamus* is also clearly specialized in being somewhat higher

TABLE 4. MEASUREMENTS, IN MM, OF LOWER TEETH OF *Incamys bolivianus*.

	N	OR	$\bar{X}$	σ	V
P_4–M_3, alveolar	4	12.5–14.0	13.4		
dm_4–M_3, alveolar	2	15.5–15.9	15.7		
dm_4 anteroposterior	3	ca. 3.8–5.21	4.45		
width metalophid	3	1.94–2.43	2.10		
width hypolophid	4	2.65–2.96	2.78		
P_4 anteroposterior	22	2.97–4.24	3.67	±.32	8.72
width metalophid	20	2.14–3.09	2.64	±.24	9.09
width hypolophid	21	3.03–3.61	3.28	±.20	6.09
M_1 anteroposterior	27	2.67–3.57	3.12	±.24	7.70
width metalophid	18	2.86–3.87	3.38	±.26	7.69
width hypolophid	22	2.93–3.85	3.44	±.23	6.69
M_2 anteroposterior	25	2.65–3.51	3.19	±.25	7.84
width metalophid	19	2.78–4.15	3.55	±.35	9.86
width hypolophid	23	2.99–4.05	3.58	±.28	7.82
M_3 anteroposterior	13	2.95–3.78	3.26	±.28	8.59
revised ant. post.*	11	2.95–3.50	3.17	±.20	6.31
width metalophid	12	2.85–3.68	3.29	±.24	7.30
width hypolophid	14	2.64–3.50	2.97	±.22	7.41
I_1 anteroposterior	29	1.85–2.63	2.20	±.22	10.00
transverse	31	1.38–2.01	1.61	±.15	9.32
ratio	29	.61–.84	.73	±.05	6.85

* The anteroposterior measurements of two specimens (PU nos. 21952 and 22335) were omitted for this calculation, as the alveolus was so damaged that anteroposterior measurements were not accurate.

crowned and notably more lophate than the five-crested genera. Lavocat then argued (1976: 43) that we should agree that four-crested genera in the Deseadan should likewise be recognized as derived from something like the contemporaneous five-crested forms. But, in the Deseadan, the majority of the low crowned and clearly cuspidate genera have four-crested upper teeth (*Platypittamys*, *Deseadomys* and *Sallamys*; *Protosteiromys* is the only exception), whereas the higher crowned and lophate genera are frequently five-crested (*Cephalomys*, *Branisamys* and the unnamed genus discussed on p. 430; we do not know how many crests there were in the upper teeth of *Scotamys*). *Incamys*, with an intermediate stage in the development of hypsodonty, has upper teeth that do not show a fifth crest. As a result, Lavocat is forced to argue that all of the primitive looking Deseadan rodents are specialized, a conclusion that seems to us to make sense only if one adopts the preconceived idea that five-crested teeth are necessarily primitive—a point to which we shall return below (pp. 493–495).

According to Lavocat (1976: 42), careful observation of upper teeth of *Incamys* revealed a tubercle, distinct from the posteroloph, at the labial extremity of the latter, which he considered to be the metacone. Unfortunately, he gave no indication as to which specimens showed such a structure, and we could find no indication of its presence, either on his stereophoto (1976: Pl. 4, Fig. 1) or on any of the Princeton specimens (e.g., Fig. 18B)—or, indeed, of anything other than normal minor irregularities of the posteroloph. Lavocat also reported what he considered to be a variable and reduced metaloph lying on the anterior flank of the posteroloph. His figure of P^4 of the type (1976: Pl. 4, Fig. 1) shows what may be such a structure, well down in the deep valley; we cannot determine whether or not a similar structure is present on M^2 of the same figure. This type of structure, deep within a valley of a tooth that is evolving toward hypsodonty, is secondary, a neomorph, as indicated clearly in Recent dasyproctids (Fig. 20J), and not a degenerating metaloph. SAL 118, which Lavocat referred to *I. bolivianus*, does have a projection in this position on all teeth preserved, but this specimen represents an undescribed dasyproctid genus (p. 430).

The upper premolar is submolariform. It is more advanced in structure and larger relative to the molars than those of contemporary octodontoids, smaller relatively but somewhat more advanced structurally than those of *Cephalomys* and *Scotamys*, less advanced than that of *Branisamys*. In unworn or little worn specimens (Fig. 18B–D), the anteroloph slopes upward and a little forward from the protocone and then curves posteriorly to join the paracone near its base. Lavocat (1976: 45) noticed this condition in the type, but concluded that the difference from the situation in the molars is due to reduction, whereas we believe that the premolars of *Incamys* were in the process of molarization, and that the anteroloph was developing.

A cuspule may or may not be present at the labial end of the anteroloph; in one specimen, PU no. 20929, there is a cuspule at the base of the paraflexal notch, and in another, PU no. 20947 (Fig. 18A), at the base of the center of the anteroloph. The protocone is almost wholly subordinated in the crest. The protoloph is robust, thick, and abuts against the lingual portion of the anteroloph. The hypocone is sharply angulate lingually and slightly concave posteriorly toward the tip. It sends a blunt projection antero-externally, the mure (interpreted by Lavocat, 1976: 45, as the mesoloph), that comes into contact with both protocone and protoloph, and a smaller, pointed one that touches the posteroloph. The latter crest is expanded anteriorly at its labial end as a smoothly curving bulge in a few specimens (e.g., PU nos. 20960, 20943; Figs. 17C, 18C). A metaloph is in the process of developing, however, and this region of the tooth is in consequence extremely variable. Metaloph differentiation ranges from nil, as in the teeth just mentioned, to well developed (PU no. 21728, Fig. 17B), with all intermediate stages represented. In some specimens, e.g., PU no. 20965 (Fig. 17D), two small, angular projections extend forward from the anteroloph. The metaloph of P^4, when present, fails to reach the mure, as is also the case in the molars. The paraflexus is wide, and both it and the mesoflexus are much deeper in the middle of the tooth than are the notches that separate the paracone from the anteroloph and the metacone from the posteroloph. These notches are variable in depth; the former may or may not be deeper than the latter. The hypoflexus is well developed, extending up the crown for over half its height. As wear progresses, the spurs from the hypocone soon unite with the protoloph and posteroloph, but the separation of the anteroloph from the protoloph, on the contrary, increases. A cleft opens between these lophs, and the hypoflexus becomes confluent with the paraflexus, remaining so until about half of the tooth has been worn away. Anteroloph and protoloph then become joined labially (Fig. 18A,E), the hypoflexus remaining open until a very advanced stage of wear. Before lingual closure takes place, a parafossette is isolated when wear reaches a small isthmus that connects the anteroloph to the protoloph deep within the combined para- and hypoflexus. The mesoflexus is converted to an anteriorly curving fossette either slightly before or at about the same stage as the labial union of antero- and posteroloph. The grinding surface as a whole increases greatly in width as wear progresses, due to the marked unilateral hypsodonty (see above, p. 416), which is comparable to that occurring in *Cephalomys*. As in that genus, V for these values is high (Table 3).

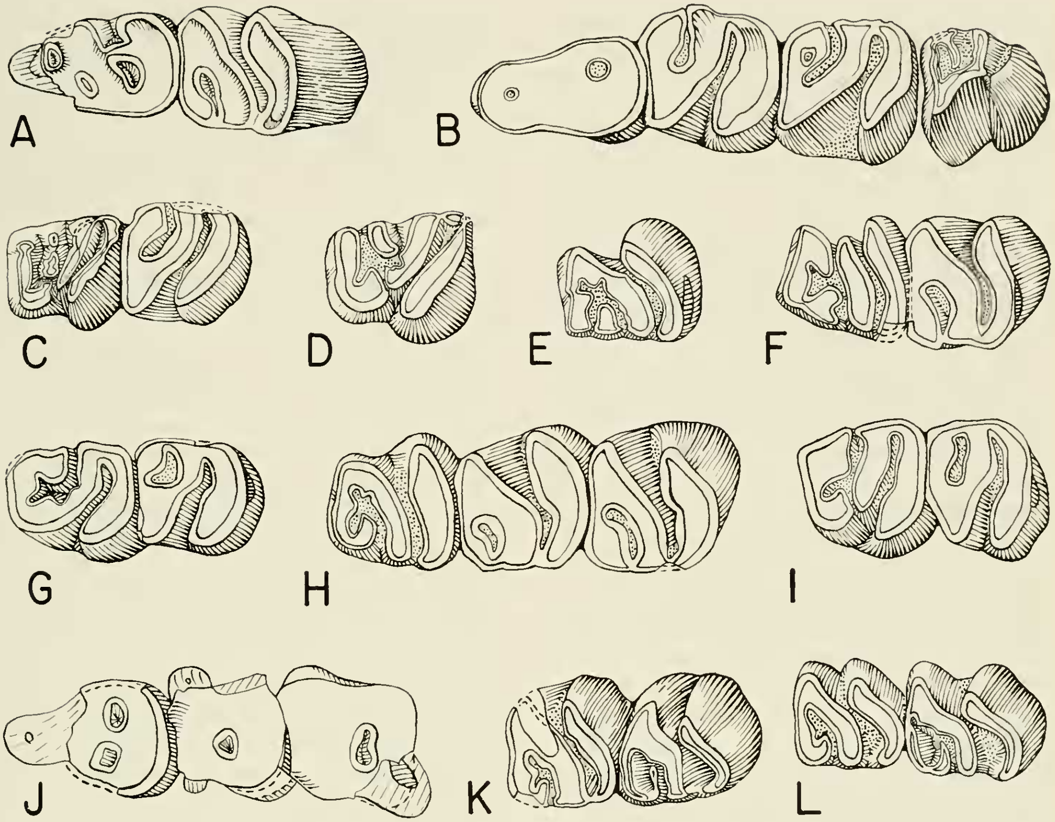

Figure 19. Lower cheek teeth of *Incamys bolivianus*, ×5. Dotted areas are matrix. A. PU no. 20921, Rdm$_4$–M$_1$. B. PU no. 21726, Ldm$_4$–M$_3$, partly restored from right side. C. PU no. 20975, LP$_4$–M$_1$. D. PU no. 20918, LP$_4$. E. PU no. 20930, RP$_4$. F. PU no. 20919, RP$_4$–M$_1$. G. PU no. 20935, LP$_4$–M$_2$. H. PU no. 20937, RP$_4$–M$_2$. I. PU no. 20948, RP$_4$–M$_1$. J. PU no. 21735, LP$_4$–M$_2$. K. PU no. 20936, RM$_{1-2}$. L. PU no. 20916, RM$_{2-3}$.

Unworn or little worn upper molars (Fig. 17A,B; Hoffstetter and Lavocat, 1970: Fig.; Lavocat, 1976: Pl. 4, Fig. 1) are approximately as long as wide at the occlusal surface and are tetralophate, sometimes with a minute projection from the anterior slope of the posteroloph of M$^{1-2}$. As in P^4, the anteroloph is usually separated from the combined protoloph and mure by a deep hypoflexus, but, in contrast to P^4, the labial notch, the paraflexus, between the two crests is very shallow (Figs. 17B, M^1; 17G, M^1 or M^2; 18A,C, M^3). The hypoflexus becomes progressively more extensive, vertically, in the posterior part of the molar series. On M^1 it extends up for approximately half the height of the crown, on M^2 rather more, and on M^3 it comes close to the base of the enamel (PU no. 20947, Fig. 18A, is exceptional in having an extensive hypoflexus on M^1). The protoloph sweeps lingually and posteriorly to the hypocone, which is also connected from the beginning of wear with the posteroloph. On the anterior face of the latter crest, a small projecting crestlet is present on M$^{1-2}$. The metaloph does not meet the protoloph. The mesoflexus has the deepest labial notch, and the metaflexal notch is almost as shallow as the paraflexal one. The metaflexus is short. Due to the shortness of the metaloph, the mesoflexus extends postero-internally to the posteroloph, joining the metaflexus. Moderate wear soon obliterates much of the detail. Paraflexus, metaflexus and crestlet disappear, the metaloph joins the posteroloph, transitorily isolating a shallow metafossette in all except PU no. 20947 (Fig. 18A), and the crown surface progressively widens. With further wear, the mesoflexus converts to an anteriorly curving fossette and a parafossette is isolated when the deeply situated isthmus connecting anteroloph and protoloph is reached, as in P^4 (Fig. 18). In the terminal stages, the hypoflexus converts to a fossette, the parafossette disappears, the mesofossette becomes irregularly pear-shaped in outline, and the convexity of the anterior faces and the concavity of the posterior ones become decidedly pronounced.

The upper cheek teeth resemble in many ways those of *Branisamys* (Figs. 23, 24). They differ in being higher crowned and shorter relative to width, in lacking neolophs, and in having shorter metalophs that fail to reach the protolophs. A basic resemblance also exists between the upper molars of *Incamys* and *Neoreomys* (Wood and Patterson, 1959: Fig. 17A), and between the upper cheek teeth of *Incamys* and *Scotamys* (Wood and Patterson, 1959: Fig. 8). Resemblances to living dasyproctids are discussed below (pp. 427–429).

The lower cheek teeth are four-crested (Fig. 19B, M_3; C, P_4; D, P_4; E, P_4; F, P_4; H, P_4; K, M_{1-2}; L, M_{2-3}). The anterior part of P_4 is longer than the posterior, as Lavocat noted (1976: 46), and the anterior part of the molars has a greater area than does the posterior. On many molars, there is a crest extending buccad from the metaconid that ends freely (Fig. 19B, M_3; K, M_{1-2}; L, M_{2-3}; Lavocat, 1976: Pl. 3, Fig. 3, M_2; Fig. 4, M_{1-2}; Fig. 6, M_1; Fig. 7, M_{1-3}). There seems to be no reason to doubt that this is the posterior arm of the metaconid that does not reach the protoconid to form a metalophid (or metalophulid II; Wood and Wilson, 1936); Lavocat (1976: 47) considers this crest to be a mesolophid, a crest with which it has not the slightest resemblance either in position, shape, or relationships.

P_4 is tetralophate, longer than the molars, and broader across the talonid than the trigonid. The anterolophid is transverse. The metalophid is variable as to size and degree of development (Fig. 19). In little worn teeth it is an independent, more or less transverse crest, but it soon becomes connected by wear to the posterior face of the metaconid. The posterior arm of the protoconid is connected, in some specimens early, in others rather late, to the hypolophid (in which the ectolophid is incorporated). The latter is joined, after slight wear, to the posterolophid, which curves antero-externally to the sharply angulate hypoconid. On eruption, the posterolophid touches the hypolophid (Fig. 19C), but the two crests separate as wear proceeds, just as do the anteroloph and protoloph of P^4. There is a small spur from the protoconid extending toward, but not fusing with, the metalophid, and there may or may not be one extending posteriorly from the center of the anterolophid. The trigonid may be somewhat twisted labially with respect to the long axis of the talonid, as in PU no. 20919 (Fig. 19F). The hypoflexid is deep and wide, extending downward nearly to the base of the enamel on the labial side. The metaflexid is confluent with it, and the metaflexidal notch is very shallow. Development of the mesoflexid is variable. In little worn specimens it crosses the tooth. Thereafter it may be closed off lingually at a rather early stage of wear or may persist until a considerably later one (cf. PU nos. 20937 and 20948, Fig. 19H–I). The anteroflexid is confluent with the deeper and larger mesoflexid, due to the separation of metalophid and protoconid. In little worn specimens there is a shallow notch between protoconid and anterolophid (cf. *Neoreomys*, Scott, 1905: Pl. 65, Fig. 9, and *Scotamys*, Wood and Patterson, 1959: Fig. 9A). With deep wear the combined anteroflexid-mesoflexid would convert to a fossettid. The hypoflexid ultimately converts to two fossettids (Fig. 19J).

The lower molars are basically tetralophate, although the metalophid is incomplete (Fig. 19). Trigonid and talonid are approximately equal in width in M_{1-2}; in M_3 the talonid is narrower (Table 4). The anterolophid is again transverse and is joined to the obliquely-running hypolophid in the unworn teeth; as in P_4, a small spur may or may not project posteriorly from it toward the posterolophid (Fig. 19B; M_3). The short transverse metalophid was apparently joined to the metaconid in the unworn state (Fig. 19B,K; Lavocat, 1976: Pl. 3, Fig. 4, Fig. 7 M_3). The large, oblique posterolophid approaches the hypolophid labially on unworn teeth (Fig. 19B), but the cleft between them widens with wear. Lingually, the two crests are separated by the shallow metaflexidal notch. The combined hypoflexid and metaflexid is large, deep, and extends nearly to the base of the enamel on the labial sides of M_{2-3}; on M_1 its extension is variable. The combined meso- and anteroflexid is comparatively shallow and of variable shape. There is a minute, ephemeral fossettid at its anterolabial extremity in one specimen (PU no. 20916, Fig. 19L). The inclination of the protoconid varies from lateral to somewhat posterolateral. After moderate wear the meso- and metaflexidal notches disappear, the lingual wall of the tooth becomes continuous, the hypoflexid widens, the metalophid loses all individuality, and the combined antero- and mesofossettid becomes slit-like; in one specimen (PU no. 21726) a small anterofossettid is briefly isolated. With deep wear the posterolophid and the hypolophid become joined by an isthmus, isolating a rounded metafossettid, the mesofossettid shortens, and the hypoflexid closes. The final stage revealed by our material is a rounded hypofossettid in an otherwise featureless crown surface, with the enamel eliminated from considerable parts of the periphery of the crown (Fig. 19J).

As in the case of the upper cheek teeth, the lowers exhibit a close resemblance to those of *Branisamys*, differing chiefly in their greater height of crown and shorter, freely projecting metalophids. Again, there is a basic resemblance to *Neoreomys* in molar structure, and a less precise one to *Cephalomys*. Comparisons with living dasyproctids are made below (pp. 427–429).

As in *Branisamys*, dm^3 was single rooted. It is a small, rather peg-like tooth, wider than long, convex anteriorly and concave posteriorly (Fig. 17A). Dm^4 (Figs. 14A; 17A,H,I) is much shorter crowned than the molars, although the degree of unilateral hypsodonty is essentially the same. In the unworn state the crown is longer relative to width than in the molars, but as wear progresses the length decreases and the width increases until, shortly before being shed, the tooth becomes square. The tooth is tetralophate, a much longer spur extending forward from the posteroloph than occurs in the molars. The anteroloph and protoloph form stout crests, the former extending posteriorly for a little over half the length of the tooth, the latter merging with the sharply angular hypocone. The metaloph fails to meet the protoloph, as in the permanent upper cheek teeth. The posteroloph continues around the labial face, where it joins the metaloph. From this portion of the crest a small spur (barely visible in PU no. 20980, Fig. 17I) projects lingually. The hypoflexus persists to within a short distance of the base of the enamel. In apparent contrast to the molars, it does not appear to be confluent with the paraflexus, the protocone and anteroloph in PU nos. 20980 and 20981 (Fig. 17H,I) giving every appearance of having joined at a very early stage of wear. The paraflexus is very large, deep and expanded anteroposteriorly. The mesoflexus, due to the incomplete metaloph, sweeps posteriorly to join the large, shallow and partially divided metafossette. Deep wear is shown by PU no. 21726 (Fig. 17A). Three fossettes, two labial and one lingual, are all that remains of the crown pattern; these are, respectively, the para-, meta-, and hypofossette.

The tooth provisionally identified by Scott (1905: 390; Pl. 65, Fig. 3) as dm^4 of *Neoreomys* is similar to that of *Incamys*, differing in the union of metaloph and protoloph, and in the presence of a small neoloph. We believe Scott's provisional identification to have been correct.

Four specimens of dm_4, all deeply worn, are available to us. They reveal that the tooth was long and narrowed anteriorly. Two preserve the last remnant of the hypoflexid and three fossettids (Fig. 19A). The posterior of these is clearly the metafossettid, and the intermediate one is presumably the mesofossettid. The anterior may be a feature of the deciduous dentition, analogous to the posterior fossettid of the trigonid of *Myoprocta*. A less worn tooth (Lavocat, 1976: Pl. 3, Fig. 3) shows four fossettids. Lavocat considered it to be essentially identical to one type of dm_4 in the early Oligocene thryonomyoid *Phiomys andrewsi* (Wood, 1968: Fig. 1G). Lavocat's figures (1976: Fig. 21,K) show that both are elongate teeth, but to us his figures strongly suggest that a more meaningful comparison could be made with dm_4 of *Cephalomys* (Fig. 26B). We find Lavocat's description somewhat difficult to interpret, especially since the pattern shown in his drawing (1976: Fig. 21) seems to differ in many respects from that shown by his stereophoto (1976: Pl. 3, Fig. 3). We continue to believe that interpretation of uncertain tooth structures in Deseadan rodents should be based on comparisons with other South American rodents and not with African ones.

The incisors are slender, rather small, and D-shaped in outline. The anterior face is more rounded in juveniles than in adults (Fig. 14C–F), particularly in the case of the lower incisors. The thick enamel extends much farther onto the lateral than onto the mesial face. The uppers extend back into the maxilla to a point slightly in front of and well above P^4. The lowers pass beneath the cheek teeth at the level of M_2 and terminate posterior and lateral to M_3. In all these respects they closely resemble the incisors of *Myoprocta acouchy*. The incisors are relatively much more slender than in *Branisamys*. The disparity in size between the incisors of PU no. 21726 (Fig. 14C,E) and those of PU nos. 20944 (Fig. 14D) and 21735 (Fig. 14F) is due to age. The first is a juvenile, the other two adults, and rodent incisors increase in diameter as growth proceeds.

Relationships. Hoffstetter and Lavocat (1970: 173) called attention to a resemblance between the lower molars of *Incamys* and those of the Fayum thryonomyoid *Gaudeamus*. Lavocat (1976) placed *Incamys* in the Dasyproctidae, but gave no reasons, and his comparisons were largely with non-dasyproctid genera, especially African thryonomyoids. The resemblance of *Incamys* to some specimens of *Gaudeamus* (although by no means to all—cf. Wood, 1968: Figs. 14, 15) exists, but this is more than offset by major differences in the premolars and in the upper molars. Affinities do not, we believe, lie in this quarter. As pointed out above, there is a very close resemblance between *Incamys* and *Branisamys* in cheek tooth structure, but differences in the skull rather definitely point to a broad rather than a narrow relationship between the two.

The known form to which *Incamys* is most closely related is beyond doubt the Santacruzian *Scleromys* (Scott, 1905: 401–403, Pl. 65, Figs. 13–15), as Hoffstetter (1968: 1096) originally believed. The two resemble each other closely insofar as they can be compared. In both, the incisors are relatively small, the patterns of upper and lower cheek teeth are very close at comparable stages of wear, and the tooth rows are nearly parallel. The snouts are similar as regards parallel-sidedness, position of the premaxillary-maxillary suture in relation to the very large incisive foramina, and the size and relations of the fossae for *M. buccinator*. *Scleromys* differs from *Incamys* in having cheek teeth that are somewhat longer anteroposteriorly, a snout that is longer relative to the length of the cheek-tooth row, and a relatively wider palate that lacks a groove running back from the incisive foramina, and is somewhat less excavated posteriorly by the choanae. These distinctions are such as might be expected between earlier and later closely related forms, and do not, in themselves, rule out the possibility of ancestor-descendant relationships.

As we have previously intimated (1959: 328), we do not believe that the Colombian Friasian species, *schurmanni* and *colombianus*, placed in *Scleromys* by Fields (1957), really belong to it. As he pointed out, they resemble dinomyids in various features, and we believe they should be placed in that family. *Scleromys* was a dasyproctid. The Colombian species may for the present be referred, with a large query, to the Patagonian Friasian dinomyid *Simplimus* Ameghino. The type species, *S. indivisus*, is larger than the Colombian ones, but poorly known. Nevertheless, the various cheek teeth figured by Kraglievich (1930c: Figs. 2, 4) agree in structure with stages of wear in *colombianus* revealed by Fields' sections (cf. Kraglievich, Fig. 2 with Fields, Fig. 14, P^4 at stage 2; his Fig. 4, center, with Fields, Fig. 14, P^4 at stage 5; and his Fig. 4, left, with Fields, Fig. 14, P_4 at stage 1). The femoral and tibial fragments, the calcaneum, and the astragalus referred by Kraglievich (1930c: Pl. 1) to *Simplimus indivisus* may represent another dinomyid. They are disproportionately large relative to cheek-tooth size, much more so than in *S. colombianus* and *Drytomomys*.

Stirton's record (1953: 61) of *Scleromys?* from the Coyaima faunule of Colombia is very dubious. Neither the generic identification nor the Colhuehuapian age assigned to the deposit can be regarded as established.

Most of the extinct dasyproctids so far discovered were neither involved in nor near to the ancestry of the surviving forms. *Cephalomys*, *Litodontomys* and *Olenopsis* (if they are correctly placed here) would appear to represent side branches (Wood and Patterson, 1959: Fig. 12). *Neoreomys*, the best known of the extinct dasyproctids, is clearly a member of a lineage pursuing an evolutionary path that was not heading in the direction of *Dasyprocta* and *Myoprocta*. *Incamys* and *Scleromys*, however, appear to us to be close to the ancestry of the living genera.

This is particularly evident in the cheek teeth (Fig. 20). Worn uppers and lowers of the living forms display a short hypoflexus and hypoflexid and an almost bewildering array of small fossettes and fossettids (Fig. 20E,F), patterns which at first glance seem almost to defy interpretation. Examination of freshly erupted or unerupted teeth, however, reveals simpler patterns (Fig. 20A–D,G–I) that basically resemble those of *Incamys* (Fig. 17B–D), and which clearly show the S-arrangement of the lophs and lophids that occurs in that form and in *Scleromys* (see Hagmann, 1907: Figs. 25–26 for the same pattern in *Dasyprocta*). The profusion of fossettes and fossettids that characterizes worn *Dasyprocta* and *Myoprocta* cheek teeth comes about not so much from structures at the apex of the tooth, as from variable projections and pillars that arise at various depths within the tooth, from the surrounding enamel walls of the lophs and lophids and also, independently it would seem, from the bottoms of valleys (Fig. 20J and Hagmann, 1907: Pl. 26, Fig. 9). A neoloph and a neolophid are present in the cheek teeth of the living species, the former arising from projections extending anteriorly from the anterior wall of the posteroloph and lingually from its antero-labial extremity; in *Incamys* the first of these is sporadically present. (Here is clear evidence, we believe, of a neoloph arising within one lineage of a family after the same crest had come into existence in two other lineages, those of *Cephalomys* and of *Neoreomys.*) The neolophid appears to arise from the base of the tooth and to participate in the grinding surface only after considerable wear (Hagmann, 1907: Pl. 26, Fig. 9; redrawn here as Fig. 20J). Upper cheek teeth of *Dasyprocta* and *Myoprocta* are longer anteroposteriorly than those of *Incamys*, but those of all three increase in transverse diameter and decrease in anteroposterior as wear proceeds; the lowers also do this, but to a less marked degree. No figured specimens of *Scleromys* have unworn teeth, but the teeth plainly show the S-configuration and are intermediate in length between those of *Incamys* and those of the living species (Scott, 1905: Pl. 65, Figs. 13–15). No other known extinct dasyproctid resembles the living species as closely as do these two in molar structure.

As concerns the skull, there are various resemblances between *Incamys* and the surviving forms. These are described in detail above. The more striking are the general shape of the skull in lateral view, the large orbits with their posteriorly situated postorbital processes, and the nearly parallel cheek tooth rows.

The resemblances are, of course, accompanied by an array of differences, as is only to be expected when comparing an early Oligocene form with living ones. The majority of these differences seem to be characters primitive for the Caviomorpha. In this category are: 1), the flatness of the cranial roof; 2), the relative shortness of the snout; 3), the more abruptly projecting anterior root of the zygoma; 4), the great posterior extension of the nasals and ascending processes of the premaxillaries; 5), the very large incisive foramina, the groove running back from them, and the associated wide separation of the fossae for the *Mm. buccinatores*; 6), the less arched occiput; and 7), the relatively slight dorsal extension of the supraoccipital at the center. Of these, 1) to 3) are present in *Cephalomys, Branisamys*, and *Platypittamys*; 4) occurs in *Cephalomys* and *Branisamys*, but not in *Platypittamys. Franimys* and *Protoptychus* have this character very well developed, however; *Platypittamys*—and the octodontoids generally—may have shortened these elements early. Character 5) is shared with *Cephalomys* and also with *Protoptychus. Platypittamys* is unknown as regards this character, but Santacruzian octodontoids possess it. *Branisamys* does not, and this is perhaps an early specialization. Characters 6) and 7) occur in *Platypittamys*, and are not known for the other Deseadan genera. In features in which *Scleromys* differs from *Incamys* (p. 426), it is intermediate structurally between the latter and the living species. Cranial evolution in the lineage leading to *Dasyprocta* and *Myoprocta* has involved a considerable lengthening of the skull that has not been accompanied by a proportionate increase in the length of the cheek-tooth row. Cheek-tooth length is nearly equal to snout length in *Incamys* (99%), less in *Scleromys* (86%), and still less in *Dasyprocta* (57%). The palate of *Scleromys* is relatively wider and longer than in *Incamys*, relatively narrower and shorter than in *Dasyprocta*, and, as in the latter, lacks the anterior groove.

Incamys is distinguished, among known dasyproctids, by the relatively very large, posteriorly expanded bulla and those features related to it, namely the narrowness of the anterior portion of the basioccipital, the slight degree of inflation posterodorsal to the tympanic,

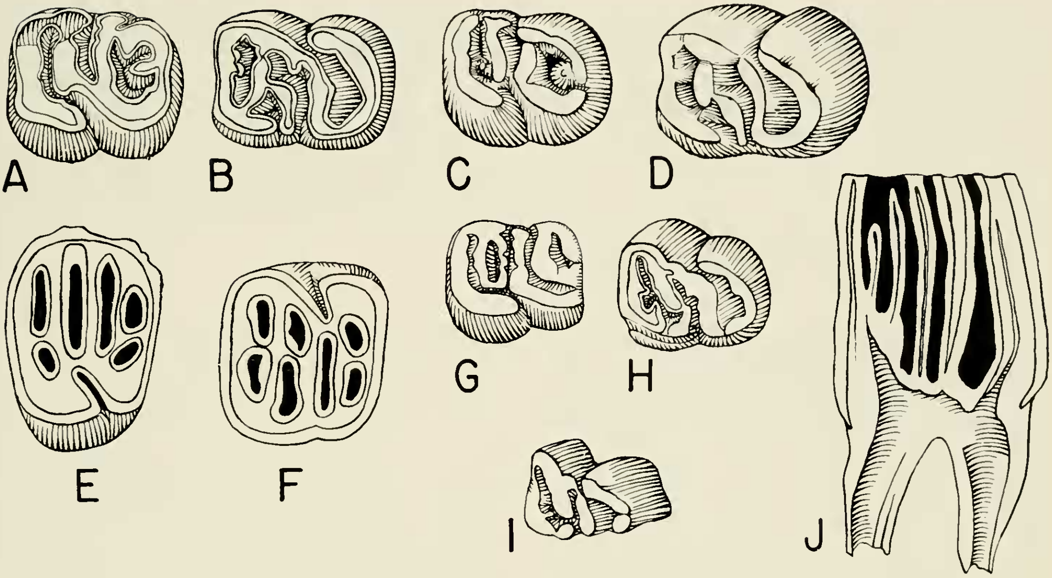

Figure 20. Molars of *Dasyprocta* and *Myoprocta*, ×5. A–D. *Dasyprocta noblei*, MCZ no. 15937. A. Worn LM^1. B. Worn RM$_1$. C. Unerupted LM^2. D. Unerupted RM$_2$. E–F. *Dasyprocta punctata isthmica*, MCZ no. 36361. E. LM^2. F. RM$_2$. G–I. *Myoprocta acouchy*. G. MCZ no. 30808, erupting LM^2. H. MCZ no. 30808, erupting RM$_2$. I. MCZ no. 30805, unerupted RM$_3$. J. Vertical section of (unspecified) lower molar of *Dasyprocta croconata*, redrawn from Hagmann, 1907, Pl. 26, Fig. 9. Anterior end to the left.

and, possibly, the short, non-projecting paroccipital process. This is partly a function of size. A large bulla tends to be characteristic of small rodents; in *Platypittamys*, for example, it is large although not so expanded posteriorly. (*Protoptychus* has an even larger bulla that is more posteriorly expanded and accompanied by a much greater degree of inflation in areas dorsal and posterodorsal to it; it may well have been a saltatorial adaptation.) The large size of the bulla would not rule *Incamys* out as an ancestor of the living dasyproctids, but the posterior expansion and the neighboring slight inflation are features of which not a trace is to be seen in *Dasyprocta* and *Myoprocta*. These, the presence of a "posterior postorbital process," and the peculiar interorbital fenestra incline us to suspect that while *Incamys* was close to the *Dasyprocta-Myoprocta* lineage, it lay a little to the side of it. Whether *Scleromys* was a descendant of *Incamys* or was more nearly on the main line are questions that only future discoveries can answer.

Knowledge of the upper dentition of *Incamys* permits the identification of an isolated left upper cheek tooth from the Deseadan of Patagonia that we described earlier (1959: 362, Fig. 24) as ?Dasyproctidae gen. et sp. indet. This is so close in details of structure to P^4 of *I. bolivianus*, especially to that of PU no. 21728 (Fig. 17B), as to leave no doubt at all as to generic identity, and on the evidence we cannot separate it specifically from the Bolivian species. We had previously been in some doubt as to the position of this tooth in the series, suspecting that it was too molariform in structure for a Deseadan premolar on the basis of the Patagonian evidence then available. The new Bolivian evidence conclusively shows that at least in the Dasyproctidae and Dinomyidae quite molariform premolars had evolved by Deseadan time. We thus have two rodents of this Age in common between Bolivia and Patagonia, now that *Cephalomys* has been recorded from Salla. The latter is the commonest mammal in the Patagonian Deseadan, as *Incamys* may well be in the Bolivian.

Undescribed Genus, Dasyproctidae aff. *Neoreomys*
Incamys bolivianus Lavocat, 1976, in part (*nec* Hoffstetter and Lavocat, 1970)

An incomplete right maxilla with erupting P^4 and little worn M^{1-2}, SAL 118, was identified as *I. bolivianus* by Lavocat (1976: 43–44, 45; Fig. 4B; Pl. 4, Fig. 2). He noted various differences from the mine run of specimens of that species, but regarded them as probably characterizing "une variété intraspécifique." The distinctions strike us as being of considerably higher taxonomic importance. Five, not four, lophs are present on the molars (see Fig. 1, p. 376), and the protoloph is joined to the apex of the protocone in the unworn P^4, both of which rule out reference to *Incamys*. Our series of *I. bolivianus*, considerably larger than that available to Lavocat, contains no specimen similar to SAL 118, nor any that are intermediate between it and typical *Incamys*.

The depths of the flexi and fossettes together with the early union of the protoloph and hypocone in the molars and the presence of a hypocone on P^4 forbid reference to *Cephalomys*. We are dealing, it would appear, with a hitherto unknown form. Of known dasyproctids it is closest to *Neoreomys* in molar structure, the only differences of any consequence being the more continuous, less interrupted lophs and the smaller size of the spur on the anterior slope of the posteroloph, which does not extend to the fourth crest, the neoloph (cf. Lavocat's stereophotograph with Wood and Patterson, 1959: Fig. 17A). The premolar differs in that the lophs are less obliquely directed relative to the long axis of the tooth row (cf. Scott, 1905: Pl. 65, Figs. 1–2), and a well-defined hypocone is present. The paracone sends a short spur linguad that would unite with the protoloph after very little wear; this could be an individual peculiarity.

On the scanty evidence available, we have, in SAL 118, a form that may have been close to the *Neoreomys* lineage, although not on the direct line to that genus.

Cephalomys Ameghino 1897
Cephalomys bolivianus Lavocat 1976

Cephalomys bolivianus Lavocat, 1976: 59–62; Fig. 3A; Pl. 6, Figs. 1–2.

Cephalomys, the commonest Patagonian Deseadan genus, is represented, with certainty, by one Bolivian specimen in the collection deposited in the Muséum Nationale. The type, SAL 164, consists of the ventral portion of a rostrum and most of the palate with the base of the incisor and deeply worn P^4–M^2 of both sides. As noted by Lavocat, the dimensions of the teeth fall within the size range of *C. plexus*, the smaller of the two previously known species. He gives (1976: 59) as diagnostic features the wedge shape ("en coin") of the rostrum, the very slight degree of posterior divergence of the cheek-tooth rows and the absence of an infraorbital groove.

The first two of these characters—and the smaller size—distinguish SAL 164 from *C. arcidens*, the type species. The rostrum is unknown in *C. plexus*, but the tooth rows are more divergent than in the Bolivian specimen. The reported absence of the groove (presumably for the infraorbital nerve and blood-vessels) may be more apparent than real. This is shallow in *C. plexus*, in which it is bounded laterally by a slight elevation on the side of the maxilla (Wood and Patterson, 1959: Fig. 22A). So far as can be judged from Lavocat's illustration, the type of *C. bolivianus* may have suffered some abrasion in this area, sufficient perhaps to have removed a comparable elevation had one been present. We are by no means certain that *C. bolivianus* is not a synonym of *C. plexus*, but accept it provisionally.

As noted above, the rarity of *Cephalomys* in the Bolivian Deseadan is in striking contrast to its abundance at certain Patagonian localities, precisely the reverse of the situation as regards *Incamys*.

Dasyproctidae *inc. sed.*

Genus indet., Lavocat, 1976: 68; Pl. 5, Figs. 4–5.

Two mandibular fragments, one (SAL 166) with deeply worn M_{1-3}, the other (SAL 167) with badly broken P_4–M_2, were figured and described by Lavocat, who noted some resemblances to *Cephalomys*. There is indeed a certain similarity to teeth of that form at comparable stages of wear, particularly as regards the preserved posterior portion of P_4 (cf. Lavocat, 1976: Pl. 5, Fig. 5 and Wood and Patterson, 1959: Fig. 18B). The molars of SAL 166 are so deeply worn that the mesoflexids are represented only by undulations on the lingual surfaces, yet a minute remnant of the anterofossettid of M_2 and of the metafossettid of M_3 still remain. In the Patagonian species of *Cephalomys* all traces of these would have been lost at much earlier stages of wear.

It is conceivable that these specimens might be referable to *C. bolivianus*, with which they agree in size, but it is impossible to be certain on such material.

Family DINOMYIDAE Alston 1876

Branisamys Hoffstetter and Lavocat 1970

Synonym. Villarroelomys Hartenberger 1975.

Emended Diagnosis. Skull, so far as known, basically dinomyid. Snout heavy, ventral side of rostrum elevated as in some dinomyids, less so than in *Dinomys*; fossa for origin of *M. masseter medialis, pars anterior* very deep, markedly excavated dorsally; nasals wide anteriorly, tapering gradually posteriorly, longer than in *Dinomys*, extending back over M^1. Posterior ends of nasals and premaxillae forming nearly straight line across top of skull. Interpremaxillary foramen half way back on mid-ventral surface of premaxilla, small, round, not slit-like. Premaxillary-maxillary suture crossing palate at rear of short, broad incisive foramina. Strong vertical ridge near front of lacrimal. Posterior palatine foramina beside M^1, entirely within palatine. Anterior end of palatine reaching forward to posterior end of P^4. Posterior margin of palate with small median process as in Paramyidae and Reithroparamyidae. Cheek-tooth rows divergent posteriorly. Knob for *M. masseter superficialis* on ventral surface of zygoma, as in *Dinomys*. Dental formula I_1^1, P_1^1, M_3^3, dm_1^2; incisors with flat anterior faces, robust but smaller and narrower relative to cheek teeth than in later dinomyids, gently rounded anteriorly. Base of upper incisor above P^4. Single rooted dm^3 present; dm^4 and P_4^4 essentially molariform, P^4 with low metaloph; dm_4 with highly complex anterior portion. Cheek teeth low crowned with incipient unilateral hypsodonty, lingual in upper teeth, labial in lowers. Cheek teeth slightly longer than wide when little worn, becoming wider than long with wear. Anteroloph of upper cheek teeth isolated in early stages of wear; remaining lophs uniting early and converging posterointernally on hypocone. Lower cheek teeth with posterolophid isolated in early stages of wear, remaining lophids uniting early and converging anteroexternally on protoconid.

Type Species. Branisamys luribayensis Hoffstetter and Lavocat 1970.

Distribution. Deseadan Oligocene of Bolivia.

Branisamys luribayensis Hoffstetter and Lavocat 1970
Figures 21–25

Synonym. Villarroelomys bolivianus Hartenberger 1975.

Diagnosis. As for the genus. Tooth measurements as given in Tables 5–6.

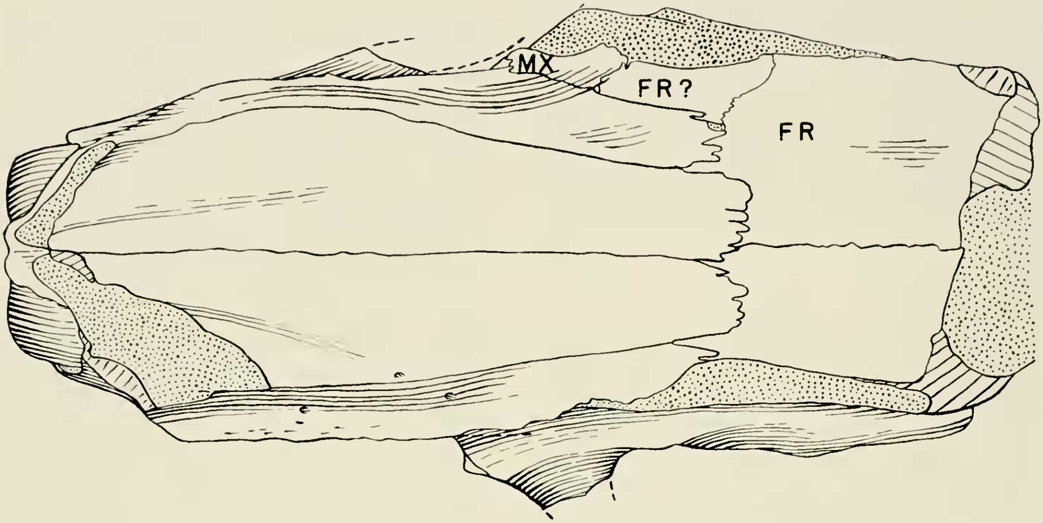

Figure 21. Dorsal view of skull of *Branisamys luribayensis*, PU no. 20914, ×3.

Abbreviations: FR—frontal; FR?—probable process of frontal, with crack between it and frontal; MX—ascending process of maxillary. Dotted areas are matrix.

Type. Portion of skull with root of dm^3, dm^4–M^3 right, cited without museum number or museum location by Hoffstetter and Lavocat (1970: 172), and as SAL 102, without museum designation, by Lavocat (1976: 33).

Type of Synonym. An incomplete Ldm_4, GB 014.

Referred Material. 31 specimens in the MNHN and Princeton collections, listed in Appendix 1 (p. 528).

Horizon and Locality. Deseadan early Oligocene, lower part of Estratos de Salla; Salla-Luribay Basin, Bolivia; all specimens are from near Salla Farm.

Description. The type is a skull missing the snout, the zygomatic arches, the occiput and part of the basicranium. Unfortunately, it has not been prepared enough to show any of the basicranial features or those of the orbit. Lavocat (1976: 34) stated that the orbitotemporal region is poorly preserved; his stereophotos (Pl. 2, Figs. 1, 3) suggest that it is still buried in matrix. Unfortunately, sutures are often impossible to identify on the photos. The Princeton skull, PU no. 20914, therefore adds considerably to our knowledge of the genus.

The rostrum is short—the length of the diastema being approximately equal to that of the cheek-tooth row (Figs. 22, 23A)—and very stout, comparable to those of *Neoreomys* and *Dinomys*, and much more robust than those of *Platypittamys*, *Cephalomys*, *Incamys* or the living dasyproctids. Dorsally, the sides are nearly parallel for most of their length but are slightly convergent anteriorly (Fig. 21); ventrally, they converge forward from the anterior roots of the zygomatic arches (Fig. 23A). The ventral surface is wide, gently rounded in the premaxillary portion and slightly concave in the maxillary portion anterior to the cheek teeth; this is probably the fossa of origin of *M. maxillolabialis.* As may be seen in side view (Fig. 22), the under side of the rostrum slopes steeply upward relative to the occlusal surface of the

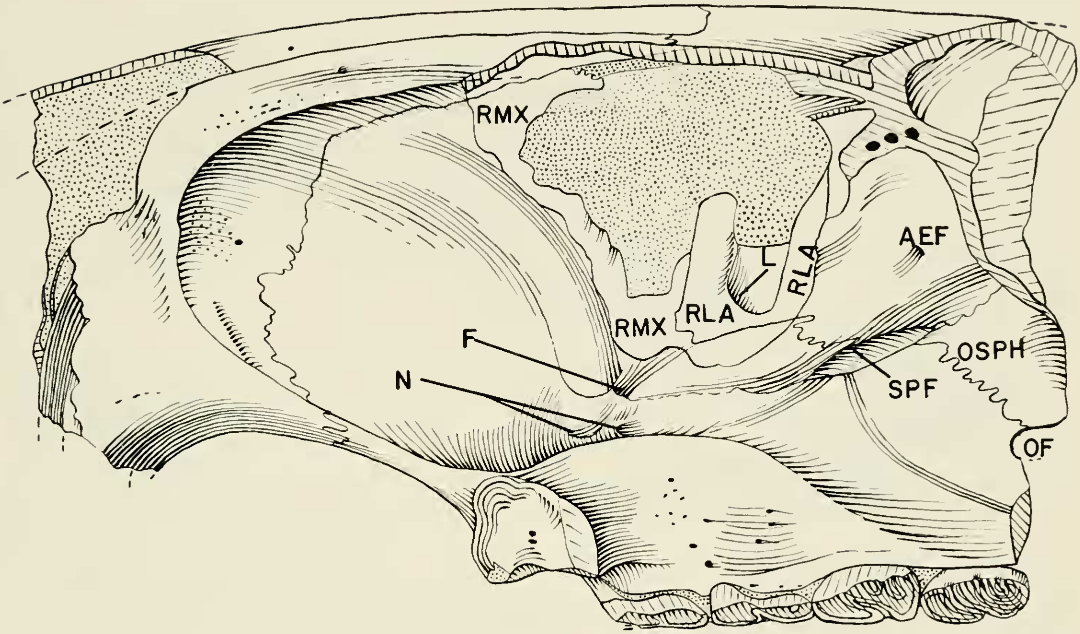

Figure 22. Lateral view of skull, *Branisamys luribayensis,* PU no. 20914, ×3. Part of orbital region restored from right side.

Abbreviations: AEF—anterior ethmoid foramen; F—foramen into nasolacrimal canal; L—lacrimal foramen; N—nutritive foramina; OF—optic foramen; OSPH—orbitosphenoid; RLA—right lacrimal, reversed from opposite side; RMX—part of right maxillary, reversed from opposite side; SPF—sphenopalatine foramen. Dotted areas are matrix.

cheek teeth, not so much as in *Dinomys* but in striking contrast to the condition in the dasyproctids. Most of the lateral surface of the snout is occupied by the very large fossa for *M. masseter medialis, pars anterior,* which extends far forward onto the premaxilla. The fossa is comparable in extent, except anterodorsally, to that of *Dinomys* but is more deeply incised and is bounded anteriorly and dorsally by a much more prominent bony rim (Fig. 22).

As in *Incamys,* the nasals are very long for caviomorphs, extending back to a point above M^1. In *Branisamys* these bones are narrow. Bluntly pointed, they increase somewhat in width posteriorly for slightly less than half their lengths and then decrease evenly toward the frontals. In contour, therefore, they resemble the shorter and wider nasals of *Dinomys,* and differ from the posteriorly tapering ones of *Neoreomys* or the more parallel-sided ones of *Incamys* and the living dasyproctids.

The premaxillaries are large and robust. Ventrally, they are relatively wider and the lateral margins are more convergent anteriorly than in *Dinomys* and, as already noted, they are more excavated laterally for the reception of the anterior portion of *M. masseter medialis.* The incisive foramina are kidney-shaped (Fig. 23A), much broader in proportion to length than in *Dinomys* or the living dasyproctids; in contrast to *Incamys* and others (p. 400), they do not extend posteriorly. The interpremaxillary foramen is small, positioned as in *Dinomys,* but is round, rather than elongate as in the living genus or in *Neoreomys.* The premaxillary-maxillary suture crosses the palate

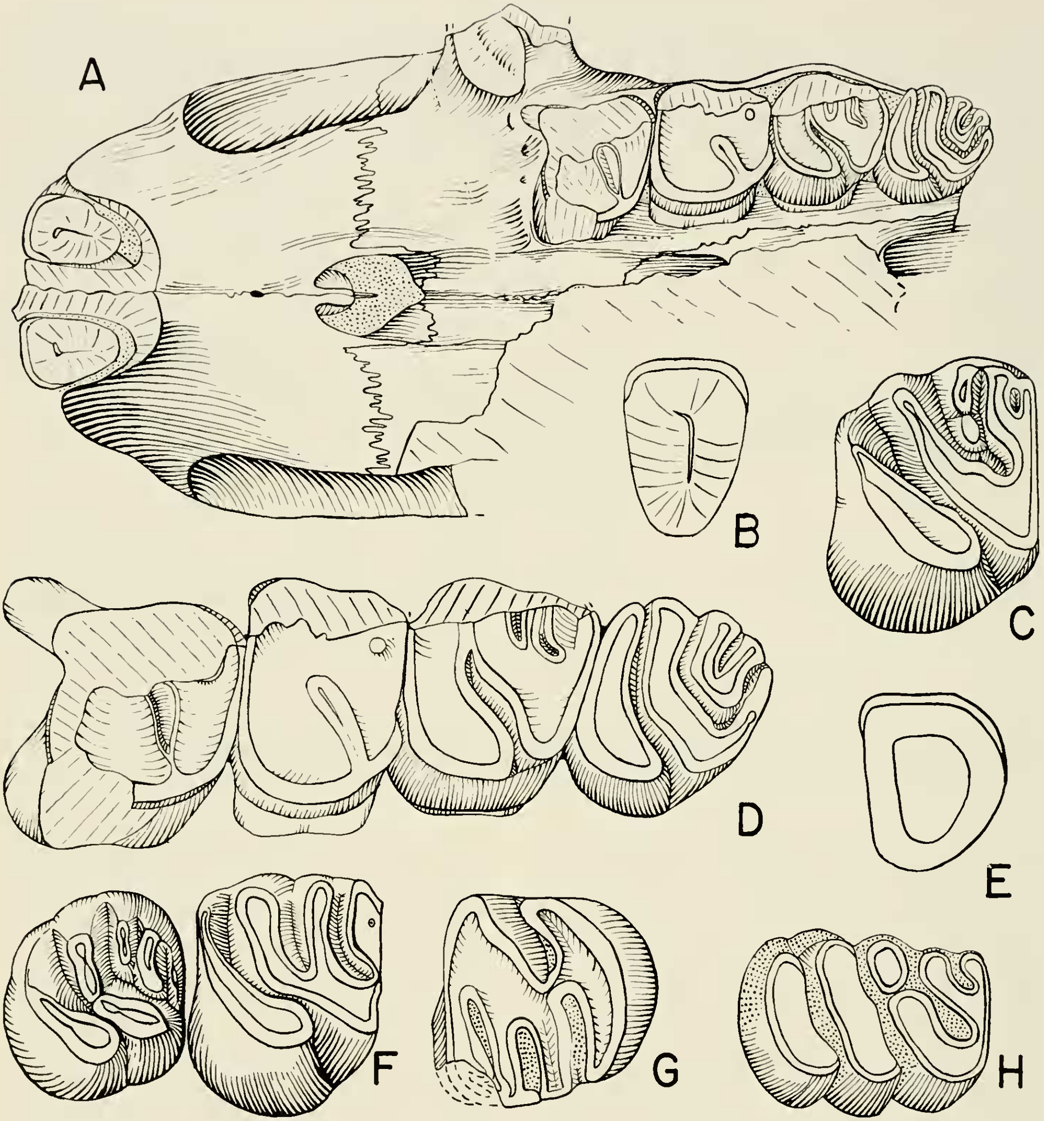

Figure 23. Skull and teeth of *Branisamys luribayensis,* and tooth of *Dinomys.* Skull, ×3, teeth, ×5. A. Ventral view of skull, PU no. 20914. Dotted areas are matrix. B. LI^1, PU no. 20914, from the front. C. LP^4, PU no. 20915. D. LP^4–M^3, PU no. 20914. E. RI$_1$, PU no. 21734, from the front. F. LP^4–M^1, PU no. 21732. G. RM$_3$, PU no. 21734. Dotted area is matrix. H. *Dinomys* sp., LM^1, AMNH (Mam.) no. 100011. Dotted areas are cement.

at the rear of the incisive foramen, then bends forward along the lateral margin of the foramen to its middle, where it turns transversely laterad across the palate, turns dorsad on the side of the snout, though with somewhat of a forward bulge that is reminiscent of the paramyids and reithroparamyids (e.g., Wood, 1962a: Figs. 2B, 13B, 48B). The positioning of the suture along the ventral surface is very like that in *Dinomys.* The dorsal process of the premaxillary extends back almost as far as the posterior end of the nasal (Fig. 21).

As in *Dinomys*, there are paired gutters along the palate, running from the incisive foramina to the posterior palatine foramina. The two gutters are separated, again as in *Dinomys*, by a median ridge, but one much lower than in the living genus. The palate narrows forward (or the cheek tooth rows converge) as in *Dinomys*. The posterior palatine foramina lie in the gutters, as in *Dinomys*, but the foramina are in the palatine, whereas in *Dinomys* they are on the maxillary-palatine suture. Our description of this area differs slightly from that of Lavocat (1976: 35). We cannot determine whether this is due to variability of this area in *Branisamys*, or whether his description is in error, since we found it impossible to trace the maxillary-palatine suture on his stereophotos (Lavocat, 1976: Pl. 2, Figs. 1, 4). Posterior to the foramina, the maxillary forms a shelf, lateral to the palatine and separating it rather widely from the alveoli of the molars.

There is a prominent rugosity for the tendon of *M. masseter superficialis* at the medial end of the zygoma. To judge from conditions in the Paramyidae and Reithroparamyidae (Wood, 1962a: Figs. 24C, 31C, 48B), this is a primitive character. As in *Dinomys*, the passage for the infraorbital nerve and blood vessels is crowded between the base of the incisor and the root of the zygomatic arch. There are two fair-sized nutritive foramina in the ventral wall of this passage (Fig. 22; N). The sphenopalatine foramen lies in the posterior part of the orbital portion of the maxilla and is touched posteriorly by the orbitosphenoid and bounded along its posterodorsal portion by the frontal. On the left side, a valley for a nerve or blood vessel runs ventrally and then posteriorly from this foramen (Fig. 22). No trace of this channel was detected on the right side.

In *Dinomys*, a small opening in the maxillary, just behind the root of the incisor, opens into the nasolacrimal canal, as can be seen by passing a flexible probe through the canal from the lacrimal foramen. This opening is very much smaller than in the later dasyproctids. There is a foramen, in *Branisamys*, just behind and below the base of the incisor, from which a faint groove extends upward and backward toward the lacrimal foramen (Fig. 22; F). Breakage on the right side shows that this foramen is continued forward in the bone, toward the nasal passage, and that it unites with another channel, running in the same general direction, which appears to be the nasolacrimal canal. This foramen would seem, then, to be homologous to the opening in *Dinomys* and to the much larger one of the later dasyproctids.

The fragmentary snout (PU no. 21960) is broken, anteriorly, at about the midpoint of the upper incisors (Fig. 25B). The incisors, inclosed in the premaxillae, have a large pulp cavity. Ventrally, the incisive alveolus is separated by a thin lamella of bone from a rounded cavity, the anterior extension of the nasolacrimal canal (Figs. 24A, 25B; NLC). The ventral portion of the premaxilla bears a V-shaped dorsal groove that houses the vomer (Fig. 25B). Between the incisive alveoli, there are at least two vertical lamellae of bone, probably portions of the turbinals, above which the nasal cavity widens (Fig. 25B; NC).

Seen from the side (Fig. 24A), the most important feature of this fragmentary snout is the nasolacrimal canal, which passes forward and ventrally from the lacrimal foramen, ventral and mesial to the base of the incisor and lateral to the nasal passage. At about the middle of the fragment, the canal enlarges and curves upward (Fig. 24A) to form a large, rounded cavity just ventral to the incisive alveoli, as seen from the front (Fig. 25B; NLC). Posteriorly, the snout is broken off just behind the cribriform plate, so that this latter is exposed from the rear. The plate is about 8.5 mm wide and 7 mm high.

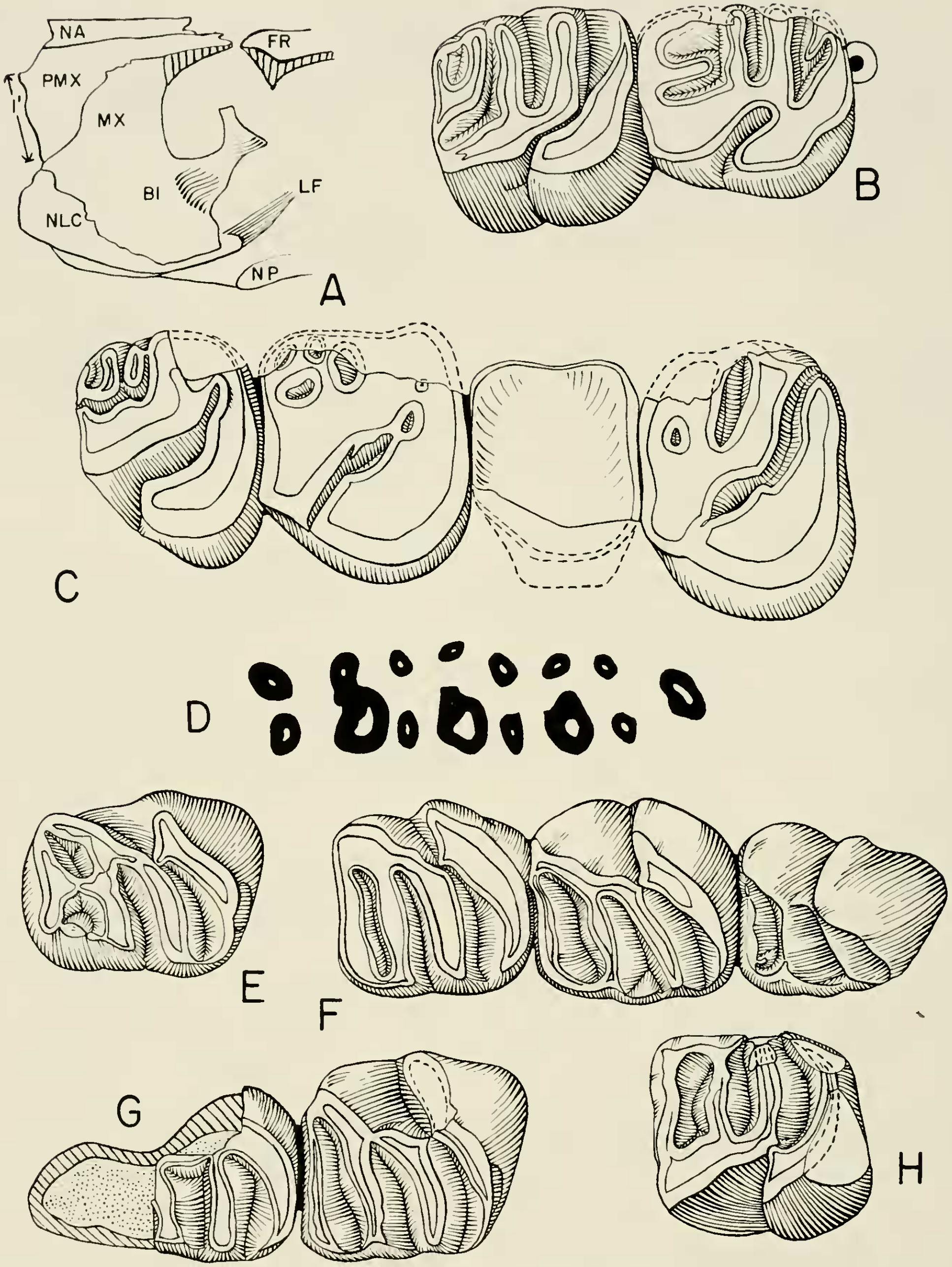

Figure 24. Snout and teeth of *Branisamys luribayensis*. Teeth, ×5; other scales as indicated. A. Ventrolateral view of snout, PU no. 21960, oriented with dorsal surface of nasal horizontal, ×2. B. PU no. 21955, Rdm^4–M^1 and root of dm^3; anterior end to the right. C. PU no. 21943, RP^4–M^3, anterior end to the right. D. Root pattern of PU no. 21978, edentulous lower jaw, ×3. E. PU no. 21980, RP_4. F. PU no. 21944, RM_{1-3}. G. PU no. 21987, broken Rdm_4 and M_1. H. PU no. 21986, LM_2.

Abbreviations: BI—base of incisor; FR—frontal; I^1—position of upper incisor; LF—lacrimal foramen; MX—maxilla; NA—nasal; NLC—nasolacrimal canal; NP—nasal passage; PMX—premaxilla.

There are relatively few, rather large olfactory foramina. There is a well-developed lamina perpendicularis, on either side of which is an elongate vertical opening.

The nasofrontal sutures are irregular; the frontals notch the nasals very slightly at the midline, and send forward small wedges between the premaxillaries and nasals (Fig. 21), as in *Cephalomys*. The Princeton specimen does not extend far enough posteriorly to determine whether or not a postorbital process was present, but one clearly was present in the type (Lavocat, 1976: 34; Pl. 2, Fig. 3). On the right side of the skull of PU no. 20914 there is a piece of bone (Fig. 21; FR?) lateral to the premaxilla and abutting anteriorly against the maxilla, from which it is separated by an obvious suture. Posteriorly, this section is separated from the frontal by either a suture or a very suture-like crack. Unfortunately this area is missing on the left side, as well as on the type. If this area is part of the frontal, as seems likely, then a projection from that bone extended forward between the premaxilla and maxilla as in *Cephalomys*, *Incamys*, and the living dasyproctids. If, on the other hand, this area is not part of the frontal but some other ossification (most likely a peculiarly shaped dorsal process of the lacrimal), the anterior edge of the frontal is almost exactly as in *Dinomys* and *Neoreomys*.

Much of the orbital portion of the frontal is present on the right side of PU no. 20914, and agrees closely, so far as preserved, with the corresponding part in *Dinomys*, being much less concave in the anteroposterior direction than in the living dasyproctids or *Neoreomys*. The ventral margin of the frontal forms a nearly horizontal line, running back from the posteroventral corner of the lacrimal to the orbitosphenoid. A good-sized anterior ethmoid foramen enters the frontal, in a posterodorsal direction, above M^3. This area has not been prepared in the type (Lavocat, 1976: Pl. 2, Figs. 1, 3).

The ventral half of the right lacrimal is present; it is very similar to that of *Dinomys*, being essentially flat and lacking any trace of the vertical plate that, in dasyproctids, connects the cranial and preorbital portions of the bone and buttresses the dorsal root of the zygomatic arch. A vertical ridge near the front of the lacrimal of *Branisamys* marks the anterior margin of the lacrimal gland just above the nasolacrimal canal. Such a ridge does not occur either in *Dinomys* or in the dasyproctids, unless, perhaps, the ridge is homologous to the initial development of the buttress of the dasyproctids.

The anterior end of the palatine, at the midline, reaches the level of the rear of P^4, a condition that is more dasyproctid than dinomyid. According to Lavocat (1976: 35) the palatines of the type reach only to the anterior quarter of M^1. The notch at the rear of the bony palate is rounded in Lavocat's figure of the type (1976: Pl. 2, Fig. 4), and lies opposite the middle of M^2; in PU no. 20914 (Fig. 23A) it clearly curved across the palate farther posterad, and there are the remains of what seems to have been a median tubercle (Fig. 23A) as in the Paramyidae, Reithroparamyidae, and *Neoreomys*, a structure not present in *Dinomys* or living dasyproctids.

The little that is preserved of the orbitosphenoid reveals that, anteriorly, it reached the posterior margin of the sphenopalatine foramen (Fig. 22), as in *Incamys* and modern dasyproctids and in contrast to the condition in *Dinomys*, and that the optic foramina were close together and confluent as in *Dinomys*, *Incamys*, and modern dasyproctids, whereas the two foramina are widely separated in *Neoreomys*.

The posterior part of the frontals and the parietals, together with the available parts of the squamosal and bulla, have been described by Lavocat (1976: 34–35).

As stated by Lavocat (1976: 35), the mandible is heavy. It is, however, not "extrêmement" robust as stated by Lavo-

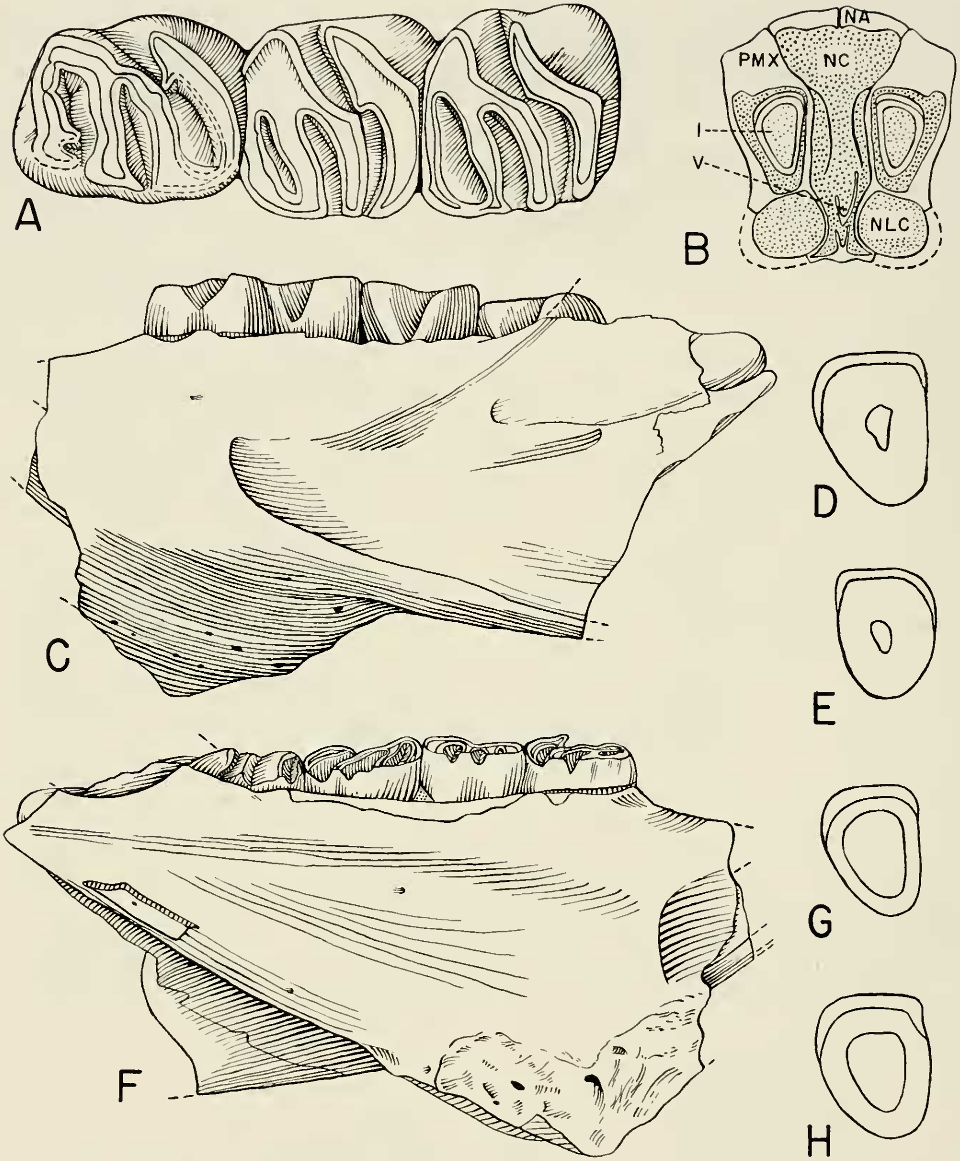

Figure 25. Snout, jaws and teeth of *Branisamys luribayensis*. Teeth, ×5; other scales as indicated. A. PU no. 21951, RP_4–M_2. B. PU no. 21960, snout broken about mid-length, seen from front. C. Lateral view of lower jaw, ×3. Largely based on left mandible, PU no. 21978, but masseteric fossa and angle completed from PU no. 21979; teeth reversed from PU nos. 21944 and 21951. D. PU no. 21978, cross section of LI_1 below diastema. E. PU no. 21944, cross section of RI_1 below anterior root of dm_4. F. Medial view of lower jaw, ×3. Based on same specimens as in C. G. PU no. 21987, cross section of RI_1 below rear of M_1, seen from the rear. H. PU no. 22172, cross section of RI_1 below rear of M_2, seen from the rear.

Abbreviations: I—cross section of incisor; NA—nasal; NC—nasal cavity; NLC—nasolacrimal canal; PMX—premaxilla; V—vomer. ×2.

cat, nor anywhere near so heavy as it would appear in his figures (1976: Pl. 2, Figs. 5–7), in which the jaw was photographed perpendicular to the occlusal surface. As in all caviomorphs, if the jaw is oriented in its natural position, the occlusal surface of the cheek teeth slopes down at about 30° toward the midline. When photographed perpendicularly to the occlusal surface, the medial surface of the jaw, which was vertical in life, appears as a broad medial shelf (Lavocat, 1976: Pl. 2, Figs. 5–7). Anteriorly, our specimens are all broken farther to the rear than is SAL 105 (Lavocat, 1976: Pl. 2, Fig. 6) and show nothing of the length of the diastema (Fig. 25C,F). However, his photograph looks as though the incisor had been pushed to the rear in SAL 105, greatly shortening the diastema. There is a deep and very narrow groove on the ventral surface of the mandible between the incisive alveolus and the angular process, which seems to differ from what Lavocat saw, since he said (1976: 35) that the groove was "large et profond." However, his stereophoto (1976: Pl. 1, Fig. 6) shows that the matrix had not been removed from this region before the specimen was photographed. There is a prominent chin process (Fig. 25C) on which there are a number of nutritive foramina. There is no trace in any of the Princeton specimens of a mental foramen (Fig. 25C; the small foramen beneath P_4 in PU no. 21978 faces backward and cannot be a normal mental foramen), which would seem to indicate that the foramen was farther forward than in *Dinomys* (Ellerman, 1940: Fig. 41). Lavocat neither figures nor mentions a mental foramen. The dorsal border of the masseteric fossa is clearly marked and is continued into the coronoid process, which passes the alveolar border by the talonid of M_3. There are a number of suggestions of subdivision within the masseteric fossa (Fig. 25C), among which the insertion of *M. masseter medialis, pars posterior* (Woods, 1972: 128, Fig. 3A) is the most prominent.

On the medial surface of the mandible, the chin process, behind the symphysis, is highly corrugated (Fig. 25F). There is a distinct cavity, above the corrugated area and in front of P_4, which may represent the fossa for an unusually large *M. genioglossus*. This view of the jaw shows the position of the deep groove between the incisive alveolus and the angular process.

At the time of its description, the type provided, for the first time among Deseadan caviomorphs, some evidence of the upper deciduous dentition (Hoffstetter and Lavocat, 1970: Fig.; Lavocat, 1976: 36, Pl. 2, Fig. 4), but it is no longer unique, as the upper deciduous dentition of *Incamys* is now known (see above, p. 425) and dm^4 and the root of dm^3 of *Branisamys* are present in PU no. 21955 (Fig. 24B). This specimen and the type preserve the single root of a very small tooth in front of dm^4 (for a discussion of the precise nature of the tooth in front of dm^4 or P^4, see Wood, 1969; 1970b: 245–246). In the adult Princeton specimens there is no trace of such an alveolus, the maxilla sloping upward from the anterior border of the alveolus of P^4 with no indication of an anterior alveolus, unless what seem, in PU no. 20914, to be nutritive foramina represent the last stage in the filling of the alveolus with replacement bone, as occurs in the European paramyid *Plesiarctomys* (Wood, 1970b: 245, Fig. 8), and, possibly, in *Sallamys* (p. 383). However, there are definite nutritive foramina in this position in, e.g., *Erethizon*, in which neither dm^3 nor P^3 is ever present (Wood and Patterson, 1959: 378). The areas in front of P^4 in PU nos. 20915, 21732, 21733, and 21943 show no nutritive foramina and no suggestion of an alveolus.

The functional upper cheek teeth are basically low crowned, although unilateral hypsodonty has begun to develop on

TABLE 5. MEASUREMENTS, IN MM, OF UPPER TEETH OF *Branisamys luribayensis*.

PU nos.	20914		20915	21732	21733	21943	21955	21960		
	L	R	L	L	R	R	R	L	N	X̄
P^4–M^3 anteroposterior	20.8					20.9			2	20.85
dm^4 anteroposterior							5.83		1	
width metaloph							5.00		1	
P^4 anteroposterior	5.20		5.50	4.68	4.53	5.53			5	5.09
width protoloph			6.82	5.18	5.05	7.30			4	6.09
width metaloph			6.29	5.24	6.15				3	5.89
M^1 anteroposterior	4.34			4.88	4.85	4.45	5.40		5	4.78
width protoloph	ca. 5.9			6.45	6.30		5.92		4	6.14
width metaloph				5.83	5.40		5.83		3	5.69
M^2 anteroposterior	5.05					5.57			2	5.31
width protoloph	ca. 6.0								1	6.0
M^3 anteroposterior	4.82					4.98			2	4.90
width protoloph	5.44								1	5.44
width metaloph	5.30					5.14			2	5.22
I^1 anteroposterior	4.9							4.21	2	4.56
transverse	3.32	3.24						3.14	3	3.23
ratio	.68							.75	2	.71

the lingual side. Lavocat (1976: 36) compares this condition to that in the Miocene *Paraphiomys pigotti* of Africa. There is no question but that the two are at comparable stages of evolution of unilateral hypsodonty. However, the same may be said for many other rodents (paramyids, reithroparamyids, theridomyids, prosciurines, ischyromyids and cylindrodonts, to name a few selected at random from the early Tertiary). All that this indicates is that unilateral hypsodonty is very common in the upper cheek teeth of rodents—and lagomorphs as well (Wood, 1942: 4, Table p. 5). Unilateral hypsodonty has absolutely no weight as an indication of caviomorph-thryonomyoid relationships short of the ordinal level. The degree of lingual hypsodonty in *Branisamys* is no greater, proportionately, than in most paramyids and reithroparamyids. Enamel was continuous around the crown until late stages of wear (Figs. 23D, 24C, rear of M^1), and there does not seem to have been very much interdental wear. The teeth are somewhat wider than long for most of their lifetime, but in the early stages of wear the grinding surfaces are rather longer than wide (Table 5). This change takes place through the progressive widening of the wear surface down the lingual slope of the protocone and hypocone, but the change is not so prominent as in *Incamys*.

All upper cheek teeth are five-crested (Figs. 23C,D,F; 24B,C; Lavocat, 1976: Pl. 2, Fig. 4), having a small fourth crest, the neoloph, that attaches to the anterior face of the fifth crest, the posteroloph, near its middle. For terminology of the parts of the cheek teeth, see Figs. 1–2 (pp. 376–377). Each tooth overhangs posteriorly behind the hypoflexus, which results in progressive decrease in the size of the posterointernal corner as wear proceeds. There is a slight tendency for the enamel to be thicker on some of the anterior than on some of the posterior faces of the lophs, a tendency carried much farther in *Dinomys*. Cement is lacking on all teeth.

Little worn teeth are preserved in PU nos. 20915, 21732, 21733, 21943 and 21955. P^4 is almost, but not quite, fully molariform. Protocone and anteroloph together form a stout crest, bulging anterolingually (Fig. 23C,F), that extends from the posterolingual portion of the crown around most of the anterior face, falling short of the paracone. Paraflexus and hypoflexus are confluent through much of the depth of the crown, effectively isolating this anterior crest until an advanced stage of wear (Figs. 23A, 24C). The protoloph, thus separated from the protocone, extends obliquely from the paracone to the hypocone. In early wear stages (Fig. 23F) the two cusps are separate. The mure, as such, has lost all individuality. The neoloph is a short crest that joins the center of the posteroloph after a little wear. Labially, it soon fuses with the posteroloph to isolate a small, ephemeral neofossette. The "metaloph" is the last of the crests to come into wear. Although we employ the same names for structures on premolars as for the topographically corresponding ones on the molars, it is nevertheless quite clear that the metaloph has had different histories in the two sets of teeth (p. 386). It is closest to the wear surface labially where it approaches the neoloph, from which it is separated by a slight notch, and then makes contact far dorsal to the grinding surface with a bulge on the labial side of the protoloph. Midway in its course, the metaloph is slightly constricted from below and from the sides, and these constrictions give it a fleetingly bicuspidate structure. The combined para- and hypoflexus and the mesoflexus extend to within short distances of the base of the enamel. The small neoflexus, which is open labially only in the earliest stages of wear (Fig. 23F), is the shallowest of the crown features, and disappears after a small amount of wear (Fig. 24C). This is the most advanced P^4 yet reported from Deseadan rodents. The premolars of PU nos. 21732 and 21733 have different measurements and are smaller than those of the other specimens (Table 5) because the teeth are not fully erupted.

The molars differ from P^4 primarily in the more buccal extension of the anteroloph, in their greater length on eruption (Fig. 24B) and in the more nearly central position of the lingual opening of the hypoflexus, again on eruption (Fig. 24B). The length rapidly decreases with wear. The three posterior lophs are variable in their connections. M^1 and M^3 of the type resemble P^4 of PU no. 20915. In M^2 of the type, however, the central portion of the metaloph inclines posteriorly to unite with the neoloph, its normal course being marked by a buccal cuspule. This cuspule was regarded by Hoffstetter and Lavocat (1970) and by Lavocat (1976: 37) as a mesostyle. We take it to be a minor individual variant representing a secondarily isolated remnant of the metacone. Comparable metaconal isolations can be seen in little worn molars of *Dinomys*, as individual variations (Fig. 23H). The valley between the posteroloph and the neoloph is extremely shallow (Fig. 24B) and rapidly removed by wear (Fig. 23F).

In M^3 of PU no. 20914 (Fig. 23D), the metaloph and neoloph unite in an irregular V that is isolated from the protoloph and posteroloph by the combined mesoflexus and neoflexus; slight additional wear would result in a neoloph-posteroloph union. In PU no. 21943 (Fig. 24C), the posteroloph and neoloph have united, leaving a nearly isolated metacone. These variations are of no taxonomic significance; minor and inconsequential shiftings of loph connections occur with some frequency among caviomorphs. The molars of PU nos. 20914 and 21940, older individuals than the type, reveal that the combined paraflexus and hypoflexus closes from the buccal toward the lingual side, and that the metafossette is somewhat more persistent than the mesofossette. In the type, M^3 is small in comparison with the anterior teeth, which is not the case in PU nos. 20914 and 21943; this may be due to incomplete eruption of M^3 in the juvenile type. Lavocat's stereophoto (1976: Pl. 2, Fig. 4) suggests, however, that the eruption is almost complete but that the tooth is still partly buried in matrix.

There are a number of lower jaws in the Princeton collection, several being

TABLE 6. MEASUREMENTS, IN MM, OF LOWER TEETH OF *Branisamys luribayensis*.

PU nos.	21734 R	21944 R	21951 R	21978 L	21980 R	21986 L	21987 R	22172 R	22173 R	N	X̄
P_4–M_3 anteroposterior				20.55 (alv.)						1	
dm_4 anteroposterior							ca. 7.15			1	
width hypolophid							ca. 4.7			1	
P_4 anteroposterior			6.13		6.28					2	6.20
width metalophid			4.58		4.29					2	4.44
width hypolophid			4.91		5.01					2	4.96
M_1 anteroposterior		5.17	4.64				5.40			3	5.07
width metalophid		5.02	5.26				5.37			3	5.22
width hypolophid		5.21	5.47				5.43			3	5.38
M_2 anteroposterior		5.56	4.80			5.67				3	5.34
width metalophid		5.50	5.46			5.55				3	5.50
width hypolophid		5.54	5.28			5.48				3	5.43
M_3 anteroposterior	5.67	5.63								2	5.65
width metalophid	5.63	4.74								2	5.19
width hypolophid	4.93	4.30								2	4.62
I_1 anteroposterior		3.47	4.03	4.08	4.55		3.48	3.80	4.00	7	3.92
transverse		2.65	2.92	3.07	3.66		2.65	3.04	3.17	7	3.02
ratio		.76	.73	.75	.80		.76	.80	.79	7	.77

edentulous, but the dentition is well represented by PU nos. 21944 (Fig. 24F); 21951; 21987 (Fig. 24G); 21980 (Fig. 24E); 21734 (Fig. 23G); and 21986 (Fig. 24H). The edentulous jaws clearly show the root pattern (Fig. 24D), with four well-separated roots (the largest beneath the hypoconid) on P_4–M_2, but with only a single anterior root under dm_4 and a single posterior one under M_3.

Lower teeth were illustrated by Hoffstetter and Lavocat (1970; Fig.), and Lavocat described lower teeth in detail (1976: 38–40), figuring three specimens (1976: Pl. 2, Figs. 5–7). All permanent teeth are tetralophate with the enamel extending farther rootward on the buccal side, especially on the hypoconid, than on the lingual side. They are to a considerable extent mirror images of the uppers (except that the latter have five crests), the anterior three lophids uniting at the protoconid, with the posterolophid initially set apart by confluence of the hypoflexid and metaflexid; these, however, become separated at an intermediate stage of wear (Fig. 23G). Hypolophid and metalophid are separated lingually by a rather deep mesoflexid, but metalophid and anterolophid are united lingually, even in unworn teeth (Fig. 24F,G), and there is thus an anterofossettid from the beginning of wear. The metalophid is a large crest that shows no signs of reduction. Lavocat (1976: 38) identified what we term the metalophid as "un mésolophide ou bras postérieur du protoconide," which, apparently, he considered to be the same thing. They are, of course, quite different. The mesolophid is a structure derived from the mesoconid, a cusp on the ectolophid behind the protoconid. The posterior arm of the protoconid has nothing to do with the ectolophid, and runs directly linguad from the posterior part of the protoconid. If it is large enough, and reaches the metaconid, it is known as the metalophid (or metalophulid II). The presence of both a mesolophid and a posterior arm of the protoconid is clearly shown in the Egyptian *Phiomys* (Wood, 1968: Fig. 1C; 1D, M_1; 1E; 1G, M_1). Nothing of this sort has been reported in any caviomorph.

There are two specimens of P_4 in the Princeton collections; Lavocat apparently had three. The posterior half of the premolar is identical to that of the molars

(Figs. 24E, 25A). There is apparently considerable variation in the anterior half of the tooth. Lavocat stated that one specimen, referred to by him (1976: 39) as SAL 103, with P_4 in process of eruption and M_1, shows essentially the same structure in the anterior half of P_4 as do the molars. However, his photograph of SAL 103 (1976: Pl. 2, Fig. 7) shows a jaw with M_{1-3} and the roots of dm_4. This photograph is apparently of the jaw that he identified as the one referred to the holotype (1976: 33), which he stated includes a left ramus with the alveolus of dm_4 and M_{1-3} (M_3 unerupted). This is also apparently the lower jaw mentioned by Hoffstetter and Lavocat (1970: 172) as having P_4–M_3 with a length of about 20.8 mm. It clearly is *not* the right P_4–M_1 they figured (1970: Fig., B.l.Dr.). The list of referred specimens given by Lavocat (1976: 33) does include one that agrees with the 1970 figure: "P4 inférieure en éruption et M1 SAL 106." This is presumably the specimen he identified (1976: 39) as SAL 103.

In both Princeton specimens of P_4 (Figs. 24E, 25A) there is a posterior extension from the anterolophid, suggesting the rear of an anteroconid, which dams or partly dams the anterofossettid. There are also one or more lingual cusps that close or nearly close the anterofossettid lingually. Lavocat's description of this area in SAL 108 (1976: 39; unfortunately the specimen was not illustrated) is rather hard to follow, but probably indicates a tooth essentially like the two figured here. The anterior half of P_4 of SAL 105 (Lavocat, 1976: Pl. 2, Fig. 6) is completely disintegrated, and shows nothing. It is possible that Lavocat's description of this specimen (1976: 39) was written before the anterior part of the tooth was destroyed. It is unfortunate that Lavocat published no stereophotos of the jaw with P_4 in process of eruption (SAL 106?), which he stated (1976: 39) is fundamentally like the molars in its pattern. This is in accord with the drawing published by Hoffstetter and Lavocat in 1970, but we wonder whether a ridge from the anterolophid might not be present deep within the anterofossettid, far enough below the surface in the partly erupted tooth so that its presence was not noted. If so, this would make it identical to the other premolars.

Dm^4 is somewhat broken and deeply worn in the type (Hoffstetter and Lavocat, 1970: Fig., B.l.; Lavocat, 1976: Pl. 2, Fig. 4). Fortunately, a specimen in the Princeton collection is only slightly worn (Fig. 24B). Lavocat (1976: 36) stated that the pattern was clearly the same as that of the molars, which is only partially correct. The two central lophs (protoloph and metaloph) are like those of the molars. The anteroloph seems to have had a large central anterocone, and there is a posteromesially directed hook from the buccal tip of the anteroloph, being the first stage in the development of an accessory crest. From the center of the posteroloph there arises a strong, forwardly directed crest, reaching as far anteriorly as does the hypocone. A similar forward extension of the buccal end of the posteroloph lies along the buccal margin of the tooth. If the anterior ends of these two crests should join, it would result in the formation of a neoloph; we suspect that this is exactly what happened in caviomorph evolution. Nothing remotely similar to all this has been reported in any tooth of any thryonomyoid. Replacement of dm^4 did not occur until after M^3 came into full usage.

There is a small root in front of dm^4 (Fig. 24B), either that of dm^3 or of P^3. The fact that the tooth was associated with dm^4 and was lost before the eruption of P^4 in all known specimens of *Branisamys* suggests that it was dm^3. However, the tooth produced a wear facet on the dorsal slope of the anteroloph of dm^4, lay dorsal to the overhang of the anteroloph, and could not have reached the level of the occlusal surface of the upper cheek teeth. In this position, it is difficult to see

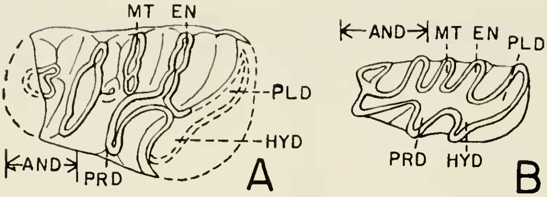

Figure 26. Tooth of *Villarroelomys bolivianus* Hartenberger compared with dm$_4$ of *Cephalomys arcidens*, ×5. A. GB no. 014 redrawn from Hartenberger, 1975: Fig. 2a, and restored according to our interpretation of its probable structure. B. Rdm$_4$ of *Cephalomys arcidens*, ACM no. 3013, redrawn and reversed from Wood and Patterson, 1959: Fig. 20A.

Abbreviations: AND—area derived from anteroconid; EN—entoconid; HYD—hypoconid; MT—metaconid; PLD—posterolophid; PRD—protoconid.

how this tooth could have erupted except after dm^4, which suggests that it might have been a P^3 that was shed along with dm^4 (Wood, 1969; 1970b: 245–246).

One badly broken dm$_4$ is present in the Princeton collection (PU no. 21987, Fig. 24G). This preserves no more than the posterior half of the pattern, which is the most molariform part of the caviomorph dm$_4$. In view of this, little more can be said of the specimen. Lavocat (1976: 39; Pl. 2, Fig. 5) described a similarly broken and more worn specimen in a ramus fragment that also includes M$_1$.

Lavocat (1976: 40–41) and Hoffstetter (1976: 10, n.) concluded that the type of *Villarroelomys bolivianus* (Hartenberger, 1975) was a dm$_4$, not an M$_3$, and suspected that it may have been a young individual of *Branisamys*, in which M$_1$ had not yet erupted. Lavocat further stated that Hartenberger was in essential agreement with him on this point (Lavocat, 1976: 40). We had independently arrived at the same conclusion. Certainly this tooth has nothing to do with the hydrochoerids. Because Lavocat felt that there was some possible uncertainty as to the reference to *Branisamys*, since the tooth of *Villarroelomys bolivianus* might represent an otherwise unknown genus closely related to *Branisamys*, he believed that the name *Villarroelomys* should be retained for the time being.

Hartenberger's illustration of the type of *Villarroelomys bolivianus* (1975: Fig. 2A) shows a tooth broken at both ends, with three crests reaching one margin, four the other, and with an assemblage of two or more cuspules near one end. The side view that he gave indicates, we believe, that the roots are somewhat divergent. This, together with the number and distribution of the crests, is convincing evidence that this tooth is Ldm$_4$ and not RM$_3$, as Hartenberger originally believed.

We have restored this tooth, from Hartenberger's illustration (Fig. 26A; our figure differs slightly, in the hypothetical portion, from the restoration given by Lavocat, 1976: Fig. 2J). There is sufficient resemblance to dm$_4$ of *Branisamys* (Fig. 24G) and to the corresponding tooth of *Cephalomys arcidens* (Fig. 26B) so that we feel considerable confidence in the general accuracy of the restoration. There are differences between GB no. 014 and Ldm$_4$ of *Cephalomys*. The Bolivian tooth is considerably larger and not quite so completely lophodont. Anterior to the metalophid, the anteroconid area of *Cephalomys* consists of an anterolingual cusp behind which there is a curved crest formed of an anterior buccal and a posterior lingual crest, whereas the anterior cusp of GB no. 014 is more isolated and is at least incipiently divided. On the other hand, the entoconid crest is shifted forward of the hypoconid-posterolophid crest as in dm$_4$ of *Cephalomys* (Fig. 26; Wood and Patterson, 1959: 340), and the central crest, which we interpreted as the metalophid in *Cephalomys*, is also as in that genus.

On the basis of its size, general appearance, and agreement with what is preserved in undoubted dm_4 of *B. luribayensis*, we feel that GB no. 014 is dm_4 of this species. It certainly cannot be referred to *Sallamys* (Fig. 5D), *Incamys* (Fig. 19A,B) or *Cephalomys bolivianus*.

The upper incisor is a robust tooth that in its course describes a semicircle extending forward from its point of origin on the medial wall of the masseteric fossa above P^4. The posterior part of the tooth bulges into the infraorbital foramen, as in *Dinomys* (AMNH Mam. no. 46551). The anteroposterior diameter is greater than the transverse, the width/length ratio being between .67 and .75. Near the wear surface, the anterior face is flat over most of the width, becoming a little rounded laterally (Fig. 23A,B). Farther back, the anterior face is more rounded, and the pulp cavity becomes very large (Fig. 25B). The tooth is much more like that of *Dinomys* than like those of dasyproctids. The enamel extends for short, nearly equal distances onto the lateral and medial faces, again as in *Dinomys*. Near the wear surface (Fig. 23B), the pulp cavity is small, and shaped like a distorted figure 7 rather than like a distorted T as in *Dinomys*. The lower incisor was generally similar (Figs. 23E; 25D,E,G; Lavocat, 1976: 36; Fig. 3E,H). The enlargement of the pulp cavity beneath the rear of M_1 of PU no. 21987 (Fig. 25G) is related to the age of the individual (dm_4 still present) rather than to the position in the jaw, as is shown by adult specimens (PU nos. 22172 and 22173, Fig. 25H) that are broken farther to the rear.

Relationships. Hoffstetter and Lavocat compared *Branisamys* with *Neoreomys*, from which they distinguished it (1970: 172) "notammement par la brachyodontie, et par la réduction de M^3, ce dernier caractère excluant des liens directs." They were entirely correct in this, and they were fully justified in comparing *Branisamys* with *Neoreomys*, which, on the basis of the cheek teeth, it closely resembles. The two forms are definitely related, although not, we believe, at the family level. Lavocat (1976) made comparisons of *Branisamys* with other Deseadan rodents, with Oligocene and Miocene African rodents, but with no post-Deseadan South American genera except *Neoreomys*, and in this instance the comparisons were limited to the cheek teeth. He concluded (1976: 73) that *Branisamys* and *Incamys* should be placed in the same family and that *Branisamys* was clearly related to *Neoreomys*.

The discussion of the cranial characteristics given above and summarized in Table 7 indicates rather different relationships for *Branisamys* from those suggested by Hoffstetter and Lavocat (1970) and Lavocat (1976). Almost all available cranial characters point toward affinities with the Dinomyidae, and suggest relationships between *Neoreomys* and the Dasyproctidae as proposed by Wood and Patterson (1959: 324–328). It is interesting to note that, in early members of these two families at least, the cranial characters give a better insight into familial relationships than do those of the cheek teeth. Table 7 demonstrates that, insofar as the characters available for *Branisamys* are concerned, ?*Simplimus* is somewhat aberrant with respect to known dinomyids, sharing more features with dasyproctids than with *Dinomys*. We give more weight to those in common with the latter, however, and follow Fields in his familial assignment. The family having been in existence since at least the beginning of the Oligocene, an early radiation within it may have taken place, giving rise to the Friasian *Simplimus*, a side line independent of the later dinomyid radiation.

Derivation of the cheek teeth of later dinomyids from those of *Branisamys*, or some similar form, would not present serious difficulties. The requirements for

TABLE 7. COMPARISONS OF *Branisamys* WITH DINOMYIDS AND DASYPROCTIDS.

	Simplimus?							
	schurmanni	*angustus*	*Drytomomys*	*Dinomys*	*Branisamys*	*Neoreomys*	*Incamys*	*Dasyprocta & Myoprocta*
Anterior face of upper incisor	nearly flat	rounded	—	flat	nearly flat	nearly flat	rounded	rounded
Enamel equally far on lateral and medial faces of I^1	no	—	—	yes	yes	yes	no	no
Rostrum	long, stout	long, slender	short, stout	short, stout	short, stout	short, slender	short, slender	very long, slender
Rostrum sloping upwards on ventral surface	no	—	—	yes	yes	yes	no	no
Fossa for masseter on rostrum very long	shorter	—	—	yes	yes	shorter	shorter	shorter
Nasals widest point	anterior	—	—	middle	middle	anterior	nearly parallel-sided	nearly parallel-sided
Fronto-maxillary suture transverse across skull	no	—	—	yes	no	yes	no	no
Orbital portion of frontal flat	rounder	—	—	yes	yes	rounder	rounder	rounder
Vertical plate of lacrimal	absent	—	—	absent	absent	present	probably present	present
Premaxillary-maxillary suture turns back behind incisive foramen	yes	straight across	straight across	yes	yes	straight across	straight across	straight across
Cheek-tooth rows converge anteriorly	very little	no	yes	yes	somewhat	yes	yes	no
Fossa for *M. buccinator*	shallow	deep	deep	shallow	shallow	deep	deep	deep
Opening into lacrimal canal through side of maxillary	no	—	—	small	perhaps; if so, small	very large	probably; if so, large	very large
Groove in bottom of infraorbital foramen for nerve and blood vessels	yes	—	yes	yes	yes	no	no	no
Incisor base	in front of P^4	—	above P^4	above front of M^1	above P^4	in front of P^4	in front of P^4	in front of P^4

this would be progressive elongation of the teeth, already foreshadowed in unworn teeth of *Branisamys*, further separation of the lophs and lophids, together with ever-increasing height of crown, culminating in the hypselodonty of the late Tertiary and Quaternary forms. The anteroloph and posteroloph are already, in *Branisamys*, well on the way to independent status, and the changes required to isolate the protoloph as the second of the dinomyid upper cheek-tooth crests would not seem to have been very profound. Due to the absence of dinomyids from the Colhuehuapian and Santacruzian of Patagonia, the details of the process remain obscure. When the dinomyid record begins again, we see in *Drytomomys*, from the La Venta local fauna of Colombia, of Friasian age, an early member of the spectacular later Tertiary dinomyid radiation.

Fields (1957: 323) referred his material of this form, correctly we believe, to Anthony's *Drytomomys aequatorialis*, but he synonymized *Drytomomys* with *Olenopsis*. As we have previously indicated (Wood and Patterson, 1959: 361, n. 21), the syntype material of Ameghino's type species, the Santacruzian *O. uncinus* (1889: 145), is partly lost, partly referable to *Neoreomys*, and partly clearly different from Fields' material. Until such time as additional specimens are found in the Santa Cruz, clearly determinable as *O. uncinus* and clearly diagnostic, we believe that the reference of other species to this genus will serve no useful purpose. We therefore retain Anthony's generic name, *Drytomomys*, for *aequatorialis*. The Pliocene *Olenopsis typicus* Scalabrini (Ameghino, 1889: 901) is not congeneric either with *O. uncinus* or with *D. aequatorialis*, and was made the type of *Paranamys* by Kraglievich (1934: 73).

The type of *D. aequatorialis* was found in Ecuador, apparently on the floor of a cave in tuffaceous rock (Anthony, 1922). On the basis of these scanty data it could have been contemporaneous either with the tuff or with the cave. Anthony decided in favor of the latter possibility, and considered the species to be Pleistocene in age. Fields (1957: 324, n. 5) discounted this. Hoffstetter (1952: 124–125) has reported that on geological grounds the tuff may be of late Tertiary age. It would therefore appear probable that the specimen had weathered out of the roof or walls of the cave, and that the deposit from which it came is approximately contemporaneous with part of the Honda Formation of Colombia.

In *Drytomomys*, there was a highly progressive development of subparallel diagonal crests in the upper molars, fully separate initially but rapidly uniting with wear along the buccal sides of the teeth. The crests of the premolar seem to have been even more independent than those of the molars. This separation of the lophs is associated with a very considerable degree of hypsodonty. The posterolophid of the lower molars of *Branisamys* is already well on the way toward separation, with the three anterior lophs joined buccally, and the two anterior united lingually as well. *Drytomomys aequatorialis* shows the same features (Fields, 1957: Fig. 16a), but again with somewhat longer independence of crests and much greater hypsodonty than in *Branisamys*. The various later dinomyids could have been derived, with relatively little difficulty, from something very similar to *Branisamys*, by way of something like *D. aequatorialis*.

For these reasons, we have no hesitation in referring *Branisamys* to the Dinomyidae (since this was written, Hartenberger, 1975, has included the genus, with a query, in this family).

The less pronounced, but still very real resemblances of *Branisamys* to the Dasyproctidae we interpret as indicating that the two families were closely related in Deseadan time. We formerly (1959: Fig. 34) showed the Superfamily Chinchilloidea as extending back to the Deseadan with two families, the Chinchillidae and Dasyproctidae, and the Heptaxodontidae, Cuniculidae and Dinomyidae as arising from the Dasyproctidae at some unknown (but perhaps mid-Tertiary) time. This must now be modified since the Dinomyidae, in the form of *Branisamys*, were already present in the Deseadan, although not far removed from a common ancestry with the Dasyproctidae. We now agree with a growing consensus that dinomyids, dasyproctids and cuniculids should be removed from the Chinchilloidea and returned to the Cavioidea. The broader affinities of all groups are discussed below and the implications for caviomorph higher taxonomy of recent comparative anatomical and karyological work are considered (pp. 509–512).

Kraglievich (1926, 1930a, 1931, 1932a) proposed no less than four families, one of them including four subfamilies, for the reception of the genera involved in the later Tertiary radiation of what we consider to have been dinomyids. Simpson (1945: 95–96), who placed these later Tertiary genera in the Heptaxodontidae, reduced Kraglievich's swollen array to three subfamilies. ?*Simplimus* is a member of Kraglievich's Potamarchinae in this scheme, and *Drytomomys* would fit without strain into his Eumegamyinae (=Dinomyinae), but *Branisamys* could not, without knowledge of intermediate stages, be fitted into any subfamily. In view of the enlarged dinomyid vistas now opened up, it would be the part of wisdom to hold subfamilial divisions in abeyance for the time being.

Caviomorpha *inc. sed.*
Luribayomys Lavocat 1976
Luribayomys masticator Lavocat 1976

Luribayomys masticator Lavocat, 1976: 64–68; Fig. 3D; Pl. 5, Figs. 1–3.

This taxon is based on a rostrum with the incisors broken off at the alveoli and with the roots of both premolars and, in part, of LM^1. For all other Deseadan rodents (except *Palmiramys*—see below, p. 449) we have some knowledge, often good, of the cheek teeth, and the taxonomy is to a large extent based upon them. *Luribayomys* stands outside this circle. It is about the size of *Sallamys*, from which it differs in incisor cross section and in the possession of a much wider rostrum. Its rostral structure would appear to separate it from the other forms—*Platypittamys*, *Incamys*, *Cephalomys*, *Branisamys*—in which this part of the anatomy is known. It is much too small to belong to either *Protosteiromys medianus* or *P. asmodeophilus*. The rooted cheek teeth exclude it from *Scotamys*. This still leaves a number of forms with which it cannot at present be compared: *Migraveramus*, *Deseadomys*, *Xylechimys*, *Litodontomys*, Dasyproctidae aff. *Neoreomys*, *Asteromys* and *Chubutomys*, aside from the possibility of its being a valid genus. It cannot even be placed as to family. For the present it must be left indeterminate, as a clear case of a *nomen vanum* (Simpson, 1945: 27).

We can only join Lavocat in the hope for a fortunate find that will include both rostrum and cheek teeth and thus permit characterization of this genus.

Palmiramys Kraglievich 1932b (by A.E.W.)
Palmiramys waltheri Kraglievich 1932b

Kraglievich (1932b: 314–316) described *Palmiramys waltheri* as a new genus and species, based on a lower jaw from the Fray Bentos Formation of Uruguay. He referred it to the Acaremyinae, then included in the Erethizontidae, but gave no figures, and his description was not very illuminating.

Mones and Ubilla (1978: 154) concluded that the Fray Bentos was Deseadan because it contained *Propachyrucos* and *Proborhyaena*, both characteristic Deseadan genera.

Mones and Castiglioni report the discovery of a drawing (1979: 78, Fig. 1), presumably of the type specimen which they state may be presumed to have been lost. This drawing accompanied the manuscript of Kraglievich's paper. Mones and Castiglioni conclude that *Palmiramys* was probably a dasyproctid.

The measurements that Kraglievich (1932b: 315) gave for the type of *Palmiramys waltheri* are very close to those of *Migraveramus beatus* (Table 1; Fig. 3). His original identification of *Palmiramys* as an acaremyine would also be in accord with its being close to *Migraveramus*. It would be difficult to visualize, however, how wear of Deseadan octodontid teeth could produce a pattern such as that figured by Mones and Castiglioni (1979: Fig. 1).

A comparison of this figure with all available illustrations of Deseadan rodents indicates that the only closely similar form is *Incamys* (cf. Figs. 16, 19 and Mones and Castiglioni, 1979: Fig. 1). Mones and Castiglioni made no specific comparisons of *Palmiramys* with *Incamys* or any other rodents. Kraglievich's original description could fit *Incamys*, but it could equally well refer to some other genus. His measurements (1932b: 315) are those of an animal half to two-thirds the size of *Incamys bolivianus*.

Palmiramys waltheri appears to have all the characteristics of a *nomen vanum*.

DISCUSSION

Conflicting Theories of the Origin of the Caviomorpha

Description and taxonomic assessment of the Bolivian Oligocene rodents having been completed, we now turn to the broader questions that involve them, their ancestors and descendants, and their relatives in other parts of the world.

There are at present two, in large part conflicting, principal hypotheses concerning the origin, interrelationships and dispersal of hystricognathous rodents. As background for what follows, these opposing concepts must again be compared.

One of them, revived in modern form by Lavocat (1969) and by Hoffstetter and Lavocat (1970), and subsequently developed by both authors severally (Hoffstetter, 1971; 1972; 1975; Lavocat, 1971a; 1973: 254–258; 1974a; 1974b; 1976: 74–84; 1981), holds that the Suborder Hystricognathi arose in Africa from waif immigrant European paramyids, possibly related to the European Theridomyidae, that had arrived in Africa in late Paleocene or earliest Eocene time (well before the evolutionary origin of the Theridomyidae). These ancestors then gave rise to the Thryonomyoidea, from which evolved, in Africa, the Bathyergoidea and, possibly, the Hystricidae (alternatively, these last arose from thryonomyoids supposed to have reached southern Asia from Africa, as waif immigrants, around the middle Eocene). The New World Infraorder Caviomorpha descended from African thryonomyoids that had been rafted, perhaps twice (if the Erethizontoidea are as distinct as Bugge has suggested), in middle Eocene time, across a then-narrower South Atlantic Ocean. The proponents of this view tend either to dismiss the awkward fact that subhystricognathous and hystricognathous Eocene rodents are known only from North (including Middle) America as an irrelevancy, or to neglect these rodents entirely. Hussain *et al.* have recently proposed an extreme version of this hypothesis (see below, pp. 504, 515).

The second hypothesis was sketched by us in 1970 and further developed by Wood (1972, 1973, 1974b, 1975a, 1977b, 1980b, 1981); we here carry it further. It holds that the Hystricognathi arose in the late Paleocene of North America as franimorph reithroparamyids. A group, or groups, of these crossed to Asia, via Beringia, early in Eocene time, and there gave rise, directly or indirectly, to the Thryonomyoidea and Hystricoidea. Another franimorph group, the cylindrodonts, reached Asia in the late Eocene, giving rise to the Tsaganomyidae in Asia and, later, to the Bathyergidae in Africa. The thryonomyoids reached Africa, as waif immigrants, from southwestern Asia during the late Eocene; the bathyergoids and hystricoids, as dry land immigrants, during pre-Burdigalian and late Miocene times, respectively. The ancestors of the Caviomorpha reached South America, as waif immigrants, from southern North America (i.e., Middle America) in middle Eocene time. McKenna (1981: 63) has proposed a possible variant in the method by which the caviomorphs reached South America from the north. The proponents of this view of things consider the North American Eocene subhystricognathous and hystricognathous rodents as very relevant indeed.

Earlier, at a time when nothing was known of North American Eocene hystricognaths and next to nothing of the paleontology of the Old World ones, we (Wood and Patterson, 1959: 419) concluded "that the Hystricomorpha and Caviomorpha have derived those characters, which they hold in common, independently and subsequent to their geographic separation." The presumed ancestors would have been relatively undifferentiated paramyids. We added: "This is extreme parallelism," which is true, but not much, if any, more than has been reported on numerous occasions among the rodents (Engesser, 1979: 41–42; Lavocat, 1951; 1954: 127; 1955: 634; Vianey-Liaud, 1972; Wood, 1935: 249; 1936b; 1947: 156–161; 1950: 90–97; 1965: 122–124; 1974b: 38–41; 1975a: 76–77; 1977a: 133–136; 1981: 82; in press a; Wood and Patterson, 1970: 631). We do not know how many of the morphological characteristics of modern hystricognaths (Wood, 1975a: Fig. 1) had been acquired by the Eocene franimorphs; certainly at least hystricognathy and hystricomorphy had been. And certainly all features that characterize modern hystricognaths did not appear simultaneously, fully developed (Wood, 1980c: 270), but must have evolved gradually and, almost certainly, independently and at different times. Dawson (1977: 197, n.) commented that the hystricognathy of the Reithroparamyidae was "'incipient' only *a posteriori*." However, as pointed out elsewhere (Wood, 1980c: 270), unless hystricognathy arose as a single genetic mutation of one sort or another, it must have been a gradual development, its initial stages barely detectable. Since hystricognathy was the first (and only universal) hystricognath character to evolve, the initial changes were presumably the result of selective pressure for lengthening the *M. pterygoideus internus*, as an adaptation to increase gnawing ability. This was followed relatively soon (but with a definite time lag) in many groups by the evolution of hystricomorphy, resulting from a similar lengthening of *M. masseter medialis*, presumably as an analogous adaptation. This same change also occurred independently in several sciurognath lines.

In this theory, the resemblances between the Old and New World hystricognaths (and, very probably, among the Thryonomyoidea, Bathyergoidea and Hystricidae) other than hystricognathy (and possibly the correlated deepening of the pterygoid fossa) and, perhaps, hystricomorphy, have all resulted from parallel evolution during the 50-odd million years since the ancestors of the Old and New World hystricognaths separated in the early Eocene.

The two hypotheses are not mutually exclusive in their entirety. They are in agreement that, so far as our present knowledge goes, all *living* hystricognathous rodents form a natural suborder, the Hystricognathi; that Old and New World hystricognaths are distinct, infraordinally; and that the thryonomyoids and caviomorphs reached Africa and South America as waif immigrants, the latter around the middle of the Eocene. Under either view, hystricognath evolution in the Old and New Worlds has gone on independently for over 40 million years.

Beyond the points just indicated, the common ground between the two viewpoints ends and disagreements begin. Discussion of the evidence bearing on these disagreements, as presented below, must range widely, from paleogeography to parasitic nematodes, from comparisons of faunas to the excruciating minutiae of molar tooth morphology. As a beginning, we will now attempt to set the stage.

First, however, perhaps a third hypothesis, that of Croizat, should be mentioned for the sake of completeness. As recently stated by him, he feels it to be a fact that the ancestors of the Hystricomorpha "negotiated [the South Atlantic] in the Cretaceous or even earlier" and, further, "At some unspecified time earlier than the beginning of the Tertiary, certain very primitive 'proto-rodents' originated in a then unitarian continent of Gondwana. When this continent split into a later South America and Africa, respectively, these 'proto-rodents,' already on the way to evolving as taxonomically definable 'hystricomorph rodents,' turned 'American' and 'African' by right of the new continental geography . . ." (1979: 251). As pointed out by Wood (1980a), the documentary evidence for this hypothesis is nonexistent.

And, finally, as some authors have pointed out, since there is evidence supporting both the African and the Middle American origin of the Caviomorpha, there is justification for adopting a noncommittal position (Simpson, 1980: 140–141; Hartenberger, 1980: 296).

Eocene Geography

According to plate tectonic reconstructions, the world in Eocene time was well on the way toward conditions now existing. The present configuration of the continents was at least foreshadowed, although the relations of land and sea and the spacing of the continents relative to each other and their interconnections, or lack of them, were in many cases significantly different (Fig. 27). South America and Africa (*cum* Arabia), which had begun to separate at about 125 m.y.b.p., were, by mid-Eocene time, separated by a South Atlantic Ocean that was some 1300 km wide at its narrowest point. Africa was isolated from Europe and Asia, and South America from North America. Middle America, the tropical portion of the continent, seems to have ended in what is now Honduras and Nicaragua. North America had a land connection with Europe at the beginning of the Eocene, which was quickly broken (Wood, 1977b: 100), and another, also of no great duration, with Asia via Beringia at the same time; the latter was re-established for a while in the latest Eocene or the early Oligocene. Europe and Asia were separated by a seaway that lasted throughout the Eocene. This was the "Uralian trough" of Patterson (1954: 192), the Turgai Strait of Thenius (1959: 107; McKenna, 1975b: Fig. 1). One result of its elimination was the "grand coupure," the long-recognized major change in Europe between the mammalian faunas of the early and middle Oligocene (Stehlin, 1909: 502–508). India and southeastern Asia were in their present positions by the middle Eocene. The whereabouts of Australia, New Guinea, and New Zealand during the Eocene are less certain—but in any event irrelevant to the present study; rodents did not reach Australia until the early Pliocene (Archer and Bartholomai, 1978: 15; Wood, in press b).

The evidence provided by Eocene mammalian faunas, so far as these are known, is in accord with such continental relationships. South America and Africa (to judge from the absence of similarities between the Eocene faunas of South America and the Fayum fauna of Africa) had long been isolated. The faunas of northern North America and Europe were closer in early Eocene time than they were ever to be again. The faunas of

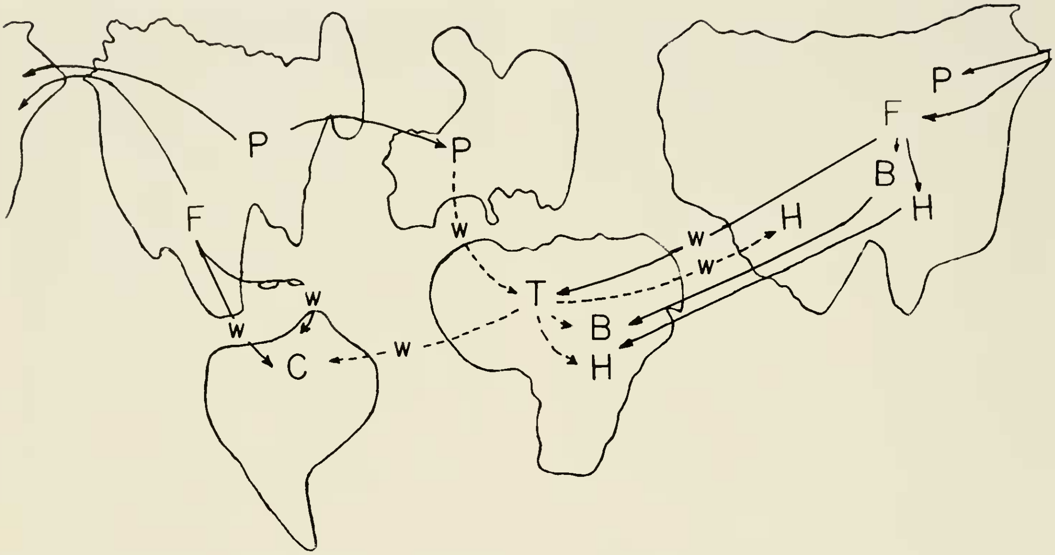

Figure 27. The world in Eocene time showing the distribution of the hystricognath groups and the Paramyidae, and the evolutionary relationships of hystricognath groups according to Lavocat (dashed lines) and according to us (solid lines). B—Bathyergoidea; C—Caviomorpha; F—Franimorpha; H—Hystricidae; P—Paramyidae; T—Thryonomyoidea; *w*—waif transport. Intercontinental migrations not marked *w* are assumed to have been via dry land. In our view bathyergids and hystricids reached Africa in early and late Miocene time, respectively.

Europe and Asia were sufficiently distinct to show that the Turgai Strait was a real barrier to interchange, whereas there were many similarities between the faunas of North America and northern Asia (Dawson, 1977).

Discoveries in the early Eocene of China of such typically Wasatchian mammals as *Homogalax* and *Heptodon*, unknown in Europe (Chow and Li, 1965), and of a paramyid in the size range of small species of *Microparamys* (Li *et al.*, 1979) strongly indicate that a connection between Asia and North America was in existence at that time. Confirmatory evidence is provided by recent finds of mammals referable to or allied with North American genera in the early Eocene Naran Bulak Formation, Mongolian People's Republic (Dashzeveg and McKenna, 1977, and references there cited). These authors point out that the presence in the Naran Bulak of *Altonius*, an omomyid of North American anaptomorphine affinities, indicates a climate in the Bering Strait region sufficiently clement to support very small primates. The Eocene, especially its earlier stages, does seem to have been a rather warm epoch.

As an aside (by B.P.), categorical statements that marsupials were absent in Asia may prove to have been premature. Didelphids reached Europe, via the North Atlantic early Eocene connection, and they could have reached Asia, via Beringia, at about the same time. Further, it is also conceivable that in late Cretaceous time they could have inhabited the river valleys of eastern Asia where they would have encountered environments similar to those of the western interior of North America, surroundings more congenial to them than the drier, more upland conditions that seem to have prevailed in Central Asia at that time.

Until very recently, all Eocene terrestrial mammals recorded from India and

Pakistan were of Holarctic affinities. There was no trace of any peculiar endemic mammals such as one might expect to have evolved on the subcontinent during its long isolation and postulated northward passage. The large mammals from the middle Eocene of Pakistan, recently described by West (1980) include a variety of cetaceans, as well as a considerable number of land mammals. These are all, with one exception, referable to Holarctic families, although generally to endemic genera. The one exception is the genus *Anthracobune*, identified by West as a primitive moeritheres, which he considered (1980: 530–531) might indicate a south Asian origin of this group. Sahni and Mishra (1975) have also reported a probable moerithere from the middle Eocene of India. No other possible descendants of the presumed south Asian Mesozoic or Paleocene mammals have been reported.

Whatever its position may have been in the Permian, the Indian subcontinent could not possibly have docked at its present position bearing a mammalian cargo of the kind revealed by its known Eocene fossils. The striking lack of endemism in the Indian-Pakistani biota as a whole is, in fact, rather difficult to reconcile with plate tectonic theory. It has been seriously suggested that the (presumed) endemic biota was essentially wiped out as a result of climatic stresses encountered during the northward passage. This strikes us as fatuous: life is more adaptable than that, and continents do not move that rapidly.

The presence of what may be primitive moeritheres in the Eocene of Pakistan and India is the only suggestion of terrestrial mammals that show any affinity to those that evolved on Africa while that continent was isolated, and it is possible that they were the ancestors of the late Eocene and Oligocene African moeritheres. The absence of other mammals of African aspect would seem to refute the idea expressed by Hoffstetter (1975: 524) that, in the Eocene, the Pakistan-Indian area was part of the African-Arabian block, and carried African hystricids to Asia. This idea perhaps was based on the then unstudied Eocene rodents of Pakistan (Hussain *et al.*, 1978). However, as indicated below (p. 504), these rodents were apparently all sciurognaths and had nothing to do with the ancestry of either the Thryonomyoidea or the Hystricidae.

Distribution of Hystricognathous Rodents in the Eocene

The Order Rodentia was certainly of northern origin. Members of it first appear in the latest Paleocene of western North America. These forms, which had already acquired all the basic ordinal characters, are referable to two very closely related families, the sciurognathous Paramyidae and the incipiently hystricognathous Reithroparamyidae, the latter, in our opinion, the ancestral stock of all later members of the Hystricognathi.

Where, in the northern hemisphere, the order arose is still uncertain. Europe would appear to have been a most unlikely place. No reithroparamyids are known from there, although Michaux (1964) referred two species to *Reithroparamys*; he later (1968: 155) made one of them the type species of *Meldimys*, a member of the sciurognathous Ailuravinae, and stated (1968: 173–174) that the other was indeterminate as to genus; both were reported only from isolated teeth, so that there was no information as to their possible hystricognathy. The paramyids that arrived in Europe at the beginning of the Eocene gave rise to a rodent fauna that evolved in isolation throughout the epoch, with a considerable variety of strictly endemic forms.

This leaves us with North America, where the early Eocene record is fairly good, or Asia, where it is not. The only early Eocene Asian rodent, so far as we are aware, is that described as *Micropar-*

amys lingchaensis from Hunan (Li *et al.*, 1979: 76), which is, we believe, a new genus and not *Microparamys*. Dr. Li informed one of us (A.E.W., April 1981) that he had reached the same conclusion and that a new name and a re-assessment of the relationships of this form are in preparation. In Figure 27 we tentatively suggest a North American origin for the rodents, but stress that an Asian one would have just about as much evidence in its favor (Hartenberger, 1980: 300). However, we believe that such an origin would not affect our thesis appreciably.

The group that, in our opinion, is the most probable ancestral stock for the rodents, the primitive primates (Wood, 1962a: 253–254), is better known in North America than in Asia. The Asiatic Eurymylidae, sometimes cited as having rodent affinities, were close to the ancestry of the lagomorphs (Wood, 1942; 1957: 417–418), but, so far as they are known at the present time, do not seem to A.E.W. to have had any special relationship to the rodents. Li (1977: 116–117) described *Heomys orientalis*, the most rodent-like eurymylid so far reported. Gingerich and Gunnell (1979: 151) cited this form as "appearing closely related to rodent origins." However, a cast of the type specimen, sent to one of us (A.E.W.) by Dr. Li, shows that the molars, particularly M^{1-2}, have a well-developed hypocone, extending linguad of the protocone, much more prominent and quite different in appearance from anything seen in primitive rodents. Whereas the hypocone of the rodents arises from the area where the posterior cingulum joins the protocone, that of *Heomys* seems to have grown from a posterior cingulum not connected with the protocone. Furthermore, the paracone is isolated from the protocone, lying behind the protoloph which is formed by the protocone, protoconule and anterior cingulum, a condition unknown among the rodents, but suggestive of the situation in early lagomorphs (Wood, 1940: Fig. 114). There apparently were a number of late Paleocene groups independently evolving gnawing incisors, at least sometimes in different geographic areas. With the evolution of the rodents, these competing lines were quickly replaced except, apparently, in restricted environments. One line, the lagomorphs, later acquired the capability of competing successfully with the rodents.

Reports of teeth identified as *Franimys*? by Sahni and Srivastava (1976: 923–924) from the middle Eocene of India, and of phiomyids or of "une famille protophiomyidée" by Lavocat (1973: 165–166) from the middle Eocene of Pakistan, are readily interpretable in terms of our view that hystricognaths were present in the Eocene of Asia—presumably these teeth had been housed in hystricognathous or subhystricognathous jaws. However, it is also possible that all of these teeth are referable to the Family Chapattimyidae of Hussain *et al.* (1978), which were members of the sciurognathous ctenodactyloids. Since the above was written, Hartenberger (1980: 288) has adopted this last point of view. Sahni (1980: 26) accepted the ctenodactyloid relationships of these forms, but considered *Chapattimys* to be a synonym of *Metkamys* Sahni and Srivastava (1976).

There obviously was extensive rodent evolution going on in Asia during the Eocene, even though we are still only barely aware of much of it. The large series of rodents described by Shevyreva (1976) is a beginning of a demonstration of this activity. The rodents that she identified as sciuravids (1968, 1971a, 1971b, 1972a, 1972b, 1972c, 1976), following Dawson's (1964: 11) tentative reference of *Advenimus* to the Sciuravidae rather than to the Ctenodactylidae, but all since transferred to the Ctenodactylidae by Wood (1977a), illustrate once more the development of hystricomorphy among sciurognaths as an occurrence independent of what happened among the hystricognaths. Quite a variety of paramyids has been reported from the Asian Eocene (Chow *et al.*, 1973: 179; Li, 1975; Li *et al.*, 1979: 79), although Hartenberger (1980: 288) considered *Yuomys* and *Microparamys lingchaensis* to be ctenodactylids. Even if Hartenberger is correct, and both of these forms are ctenodactylids, they do not seem to me (A.E.W.) to be anywhere near as distinct from paramyids as he indicated (1980: Fig. 2).

Cylindrodonts—*Ardynomys* and *Pseudocylindrodon*—had reached Asia by the late Eocene and middle Oligocene, respectively (Vinogradov and Gambarian, 1952: 14–15; Kowalski, 1974: 155–156; Shevyreva, 1976: 41–46, Fig. 16). As pointed out elsewhere (Wood, 1980b: 6; 1981: 85–87; in press a: Fig. 1), the cylindrodonts were incipiently hystricognathous (subhystricognathous). The presence of the specialized, fully hystricognathous *Tsaganomys* and its relatives in the middle Oligocene of Central Asia (Shevyreva, 1976: Fig. 16), which we recognize as a family of the Bathyergoidea (see below, pp. 515–516), and which are believed by at least one of us (A.E.W.) to have been derivatives of the subhystricognathous cylindrodonts, is an indication that much more was going on in this area.

Thryonomyoids reached Africa as waif immigrants late in the Eocene (Wood, in press b), and, we believe, unquestionably from southwestern Asia. They first appear in the record in the early Oligocene Jebel el Qatrani Formation, where they are rare faunal elements (Table 11) that had just begun their radiation. Savage (1969: 69; 1971: 220) reported rodents as being present in the late Eocene of Libya. Later he concluded (Wood, 1974b: 33) that these deposits were early Oligocene, contemporaneous with the lower level of the Jebel el Qatrani Formation of Egypt. There is no certain evidence that any non-thryonomyoid rodents were present in Africa before early Miocene time (see below, p. 467).

The caviomorphs reached South America, also as waif immigrants, in the middle Eocene (Wood, in press b). They first appear in the record in the early Oligocene Deseadan, by which time they were numerous and diversified. Had it not been for these successful landfalls on the South American and African continents, the Hystricognathi would probably now be limited to the bathyergids and hystricids, there would be no lively, widely ranging hystricognath controversy, and life on the rodent front would be duller.

Lavocat (1976: 80) believed that Eocene ocean currents would have facilitated transport of rodents on natural rafts from Africa to South America across an ocean at least 1500 km wide. He stated (1976: 61) that "diverses observations de navigateurs ne permettent pas de considérer comme infranchissable à des radeaux naturels" such a distance. Unfortunately, he gave no documentation for such "diverses observations" (Wood, 1977b: 104, n.). More recently, he has gone even farther, stating "mariners are said to have found living rodents on trees rafted as far as 2,000 km from the shores (Chaline, pers. comm.)" (Lavocat, 1978: 86). This is still anecdotal evidence, and not documentation. He and Hoffstetter (1975: 526) also believed that currents sweeping westward through the gap between North and South America would have been strong enough to have prevented rafting from the former to the latter. We know of no evidence as to the velocity of such supposed currents (see also Simpson, 1978: 326). There should, logically, be similar currents now sweeping westward between Australia and New Guinea, which do not seem to have prevented the eastward spread of Asiatic mammals, especially the Muridae, through the East Indies to New Guinea and thence to Australia.

Moreover, Lavocat's beliefs are based on the assumption that all was quiet around the Caribbean at the time, which was far from the case. Reporting on the geology of northwestern Colombia, Haffer, whose opinions carry weight due to his years of work there as a petroleum geologist, found (1970: 615–618, Fig. 6) clear evidence of two Tertiary episodes of orogenic uplift, each followed by subsidence, prior to the late Pliocene elevation of the Isthmus of Panama. It should be noted that Haffer's work was carried out in complete independence of any consideration of the South American Tertiary mammalian record, to which he did not refer. The first orogenic uplift occurred toward the end of the middle Eocene, the second toward the end of the middle Miocene. We regard it as no mere coincidence that these uplifts coincide with the presumed times of arrival of, first, rodents and primates in South America and, second, of ground sloths in North America and an extinct group of procyonids in South America.

To digress for a moment, infatuation with Africa as a source for South American Tertiary mammals has not yet embraced these raccoons, perhaps because no member of the family has ever been recorded from Africa. It has, however, extended to the hesperomyine cricetids, whose fossil record in South America dates from the end of the Pliocene. Hershkovitz (1972: 325) has suggested that the ancestors of these rodents may have been rafted across the Atlantic from Africa in the early Teriary. Satisfactory evidence of the presence of hesperomyines in North America since the late Miocene (Baskin, 1978: 131–134) disposes of this possibility, which in any event ran directly counter to the complete absence of possible hesperomyine ancestors in Africa or of any non-caviomorph rodents in the South American record prior to latest Tertiary time.

The orogenic episodes reported by Haffer are by no means all that was happening in this area. During later Cretaceous time the Caribbean-East Pacific Plate with its island arc advance guard was moving eastward between Central and South America (Malfait and Dinkelman, 1972). A partial connection through such an island arc is what would be required to account for the presence during the early Tertiary of, e.g., notoungulates in both Americas and of condylarths in South America, which last, had they been found in the north, would without hesitation have been placed in Holarctic families. Malfait and Dinkelman further concluded that, prior to the early Oligocene, the Caribbean Plate had decoupled from the East Pacific one, and that the Middle America Trench had extended south-southeastward and had become bordered along its northern flank by a chain of volcanic islands. These, following a period of quiescence, had combined by middle Miocene time to form the western portion of the present Isthmus of Panama. That these plate events bore some relation to the episodes of orogenic uplift and of subsidence reported by Haffer (whose work was evidently unknown to Malfait and Dinkelman) in extreme northwestern South America is a reasonable assumption. In other words, waif transport between the Americas would have been possible at the times that the fossil record indicates that it occurred. Ladd's views (1976) on the relation between the Americas and the Caribbean Plate do not contradict this possibility.

More recent work seems to give even stronger support to the probability that there was a Central American-Antillean land area that could well have been involved in the caviomorph migration to South America. Perfit and Heezen (1978) indicate that there was extensive uplift of Middle America from southern Mexico to include Nicaragua, as well as of the Cayman Ridge and the Nicaraguan Plateau now beneath the western Caribbean. As a result, there was deposition of a thick series of continental sediments all through this area and the Greater Antilles during the latter part of the Eocene (*op. cit.*: 1155, abstract; 1169). "Each clastic rock type appears to have a red-bed equivalent suggestive of subaerial and/or deltaic depositional environments .... The presence of plutonic clasts suggests a great deal of erosion and uplift in order to expose the [Cretaceous] intrusives by the Eocene" (*op. cit.*: 1169). Their Figure 10 indicates that there was a pre-Oligocene Cayman Ridge and Nicaraguan Plateau land mass that was continuous or nearly so from Nicaragua through Jamaica, Oriente Province of Cuba and Hispaniola. Here the rodents would have made enough easting so that they could have achieved a landfall in northern South America by island-hopping through the Lesser Antilles (either the present islands or their Eocene predecessors as suggested by Malfait and Dinkelman, 1972), crossing Lavocat's hypothetical east-to-west current from northeast to southwest (Wood, 1977b: 104; 1981: 87–88).

There seems to be a vague impression afloat that plate tectonic theory is somehow more favorable toward latest Cretaceous and earlier Cenozoic raft transport from Africa to South America than toward such transport between the Americas. If anything, as indicated above, the evidence shows that it was the other way around. Webb (1978: 395) reached conclusions similar to ours as to the distances separating South America from Africa and North (or Middle) America during the Oligocene.

If the caviomorphs, or their immediate ancestors, reached South America from the north, the place of departure of the waif emigrants was southern, or tropical, North America. Southward from the border between the United States and Mexico this portion of the continent is practically a *terra incognita* as regards its earlier Tertiary mammalian faunas. It is a large region, whose size is perhaps not always appreciated. At the beginning of the Cenozoic, its area was about half that of present-day Europe west of the USSR, and it spanned some 20° of latitude, a distance approximately equal to that between the Straits of Gibraltar and northern Scotland (Wood, 1981: 87). This area is all part of the region defined as, biogeographically, Middle America by Ferrusquía (1978: 198). Middle America "must long have been a center of adaptation and local radiation of faunal elements specifically adapted to its special conditions . . ." (Simpson, 1950: 389).

Reviewing the Recent mammalian fauna and what evidence of past ones was then available, Patterson and Pascual (1972: 255–257, Table 3) concluded that "the North American tropical peninsula was evidently a fact of ancient geography, and there is convincing Recent and suggestive Tertiary evidence that its mammals are and were distinctive to some degree within the continental fauna as a whole." Such suggestive evidence is increasing. Jacobs (1977: 518) and Baskin (1978: 133) see indications of southern elements within late Miocene rodent faunas in Arizona. Wood (1973: 32; 1974a: 102–104; 1975a: 78; 1981: 87) has concluded that rodent faunules from the middle Eocene to the early Oligocene of southwestern Texas and from the middle to late Eocene of southern California, the latter now some 200 km north of their original position due to displacement along the San Andreas rift (Merriam, 1972), were the northern representatives of a very diverse southern (Middle American) rodent fauna, quite different from the better known faunas from farther north in the western United States. All the above localities were on or near the northern fringe of the North American tropics, and have been included in Middle America by Ferrusquía (1978: 198) who placed the northern boundary of Middle America at the 35th parallel.

The only early Tertiary (probably Eocene) rodents so far found deep within Middle America, in Guanajuato, Mexico, are not like anything known elsewhere in the continent, and thus add to the growing evidence. One, *Floresomys*, may be a sciuravid, but, if so, "is a divergent member of the family" (Black and Stephens, 1973: 9); the other, *Guanajuatomys*, is a hystricognathous form that cannot at present be allocated to family (Black and Stephens, 1973: 5). Neither *Guanajuatomys* nor the likewise hystricognathous but not closely related *Prolapsus* from the middle Eocene of southwestern Texas could have been on or near the ancestry of the Caviomorpha, to judge from their cheek-tooth structure.

The Uintan *Protoptychus*, known from adjoining areas of northeastern Utah and southwestern Wyoming, was hystricomorphous and probably hystricognathous. A partial skeleton of this animal, contained in a block of hard matrix, is in the Field Museum of Natural History. The mandible, the only one known, is at present visible only in lateral view, which does not allow determination of the amount of hystricognathy that it had attained. *Protoptychus* had a tooth pattern that would have been ideally suited to have given rise to what we believe to be the primitive caviomorph type—the four-crested pattern seen in Deseadan echimyids and octodontids. We agree with Wahlert's observation (1973: 12) that the "rarity of *Protoptychus* in fossil collections supports the possibility that it, too, is based in a stock evolving elsewhere than in the western United States," which we suspect to have been in Middle America.

The earliest rodent faunas of southern California are, in general, rather similar to their contemporaries of the Rocky Mountain area, suggesting relatively little regional differentiation at that time (Golz and Lillegraven, 1977: 61 and Tables 2–3). Endemism in southern California seems to have increased fairly rapidly in the latter half of the Eocene, suggesting (Wilson, 1980: 276) that there was increased climatic differentiation at this time that led to the separation of the distinct Middle American faunas discussed above.

Berggren *et al.* (1978) have suggested that the Uintan be regarded as middle Eocene in age. The likelihood of such an age was first indicated by the discovery of *Notiotitanops*, a brontotheriid of Uintan if not Duchesnean evolutionary grade, in the marine middle Eocene Lisbon Formation in Mississippi (Gazin and Sullivan, 1942), and reinforced by Gazin's somewhat guarded observation (1955: 15) that Uintan artiodactyls were behind those of the late Eocene of Europe in their degree of advancement.

The intercalated marine and continental faunas of the San Diego area have shown that earlier Uintan continental beds are equivalent to marine middle Eocene, but that the later Uintan (equivalents of Myton or Uinta C) is upper Eocene (Golz and Lillegraven, 1977: 43 and Fig. 6). If this middle Eocene age of the earlier Uintan (Wagonhound, or Uinta A + B) be accepted, then the late early Uintan (upper Uinta B) *Protoptychus* would be middle Eocene and would have lived at approximately the time when the first caviomorphs reached South America. Some southern member or members of the Protoptychidae could have been involved in the crossing.

The recent discovery that the North American Oligocene *Cylindrodon* was at least subhystricognathous (Wood, 1980b: 6; 1981: 85–87) shows that there was another stock in the middle Eocene of Middle America (Wood, 1974a: 102–104) that may have been morphologically capable of having given rise to the Caviomorpha, although at least the Oligocene members of the family were specialized in a different direction by having acquired uniserial incisor enamel. This does not, however, seem to have been true of the middle Eocene *Mysops*, which still retained pauciserial enamel (Wahlert, 1968: 15). The middle American forms of *Mysops*, in particular, have tooth patterns that could have given rise to those of the Caviomorpha (Wood, 1973: Figs. 3–4). Unfortunately (so far as A.E.W. is aware), no specimens of *Mysops* are on record that preserve enough of the angular process to indicate whether or not this genus showed any tendencies toward hystricognathy.

There would thus seem to have been a considerable variety of hystricognathous, and, at least in part, hystricomorphous rodents inhabiting Middle America during the latter half of the Eocene. On the basis of presently available information, this area would seem to have been the center of evolution of the Franimorpha.

It is, of course, impossible for anyone to *know* what were the dental characteristics of the ancestors of the Deseadan rodents, until such forms have been found and tied in with their Deseadan descendants by a continuous series of intermediate stages. It is easy to assume that one knows, as we have done previously, and as Hoffstetter and Lavocat have also done. Since a variety of rodents is known from the Deseadan, some must be considered more primitive than others, and each author will choose those that come closest to fitting in with his opinions as to the source of the fauna. There are genera with brachyodont cheek teeth and ones with hypsodont ones; ones in which the individual cusps are clearly distinguishable from the crests, and ones in which they are not; in each case we consider the former the more primitive, but in each case we believe that Lavocat and Hoffstetter have selected the latter. The Deseadan *Platypittamys* had cheek teeth that are among the most brachyodont of any of the known Deseadan genera, and they clearly show the presence of the individual cusps. There are only four crests, with no trace of a fifth. This is the only Deseadan rodent, whose skull is known, in which the infraorbital foramen is relatively small and the masseter either did not penetrate the foramen or did so to a very limited extent. Landry (1977: 460) stated that the infraorbital foramen of *Platypittamys* was "about the same size as that of a modern *Proechimys*, and not significantly reduced as" Wood believed. A comparison of the figures of the skull of *Proechimys*, as given by Ellerman (1940: Fig. 11) and Woods (1972: Fig. 1A) shows the foramen to be considerably larger than that of *Platypittamys* (Wood, 1949: Fig. 2A). Incidentally, Wood has never believed that the infraorbital foramen of *Platypittamys* "was significantly reduced," but rather that it was primitively small. We feel that the cumulative evidence is that *Platypittamys* and the related *Migraveramus* are the closest approaches, now available to us, to conditions in the earliest South American caviomorphs.

If we are correct as to the significance of *Platypittamys* and *Migraveramus*, the pre-South American ancestry of the Caviomorpha should be sought among four-crested hystricognathous, but perhaps not yet hystricomorphous, rodents.

Summarizing to this point, Eocene subhystricognathous and hystricognathous rodents, one or more of which are rather good structural ancestors for the Caviomorpha, inhabited North (and particularly Middle) America, the only area where such rodents have so far been definitely recorded. Members of this group could have reached Asia in the early Eocene. There was an Eocene hystricognathous radiation in Middle America. There is evidence that this area has been a faunal subregion of the continent throughout the Cenozoic (Ferrusquía, 1978). Eocene geography would appear to have been such as to have permitted rafting from North to South America in middle Eocene time.

We regard such rafting of the ancestral caviomorphs (and, presumably, platyrrhines) as being distinctly easier of accomplishment than the transatlantic crossings of over 1300 km of open water postulated by Hoffstetter and Lavocat (it would seem unlikely that winds and currents would have combined to propel rafts across the shortest possible distance between Africa and South America).

Nevertheless, their views cannot be rejected out of hand. No rafting is easy of accomplishment, which is why there is evidence of so very few successful ones. A Caribbean crossing may have been somewhat less hazardous than a transatlantic one, but this does not prove that the latter could not have occurred. Nor can the possibility, envisioned by Lavocat (1973: 166), of a latest Paleocene or earliest Eocene rafting of paramyids from Europe to Africa be summarily ruled out. More recently, Lavocat (1978: 76) stated categorically that ". . . the rodents as well as at least most of the other elements of the Oligocene fauna, are probably related to animals that reached Africa much earlier, perhaps very soon after the end of the Paleocene, and probably before the Lutetian." He also said (1978: 84), referring to an early Eocene invasion of Africa by rodents, that "such an invasion necessarily did occur. . . . At least as early as the Lutetian this . . . invasion had given rise to the first Hystricognathi with all the essential characters of that group already developing." It should be stressed that there is no direct evidence for such an early Eocene or Paleocene rodent invasion of Africa, or for the presence in the middle Eocene of Africa of fully developed hystricognaths.

Successful raftings of rodents, of the kinds and at the times postulated by Lavocat and Hoffstetter, either from Europe to Africa or from Africa to South America, must have had faunal and evolutionary consequences, and this fact permits the testing of their hypotheses against the fossil record.

Had paramyids reached Africa by the beginning of the Eocene, they would certainly have radiated rapidly in that vast continent that contained no potential competition, and would have given rise by early Oligocene time to a rodent fauna at least as diversified as that of contemporary North America. The known rodents of the *early* Chadronian of North America include 23 genera belonging to 8 or 9 families (Wood, 1980b: Table 1), in contrast to the 5 genera belonging to at most 3 closely related families from the entire Oligocene of Africa. Most recently, Lavocat (1978: 84) suggested that the thryonomyoids, bathyergoids, anomalurids and pedetids were all members of the African Eocene faunas, and proposed that all of these groups shared a common stem with the Theridomyoidea. This last idea seems extraordinarily unlikely to us; the theridomyoids are a sciurognathous but hystricomorphous middle Eocene to Oligocene European group that (unless they were related to the Anomaluridae) seem to us never to have spread out of Europe. Lavocat's suggestion of a relationship of this group of families and superfamilies appears to us to be a retreat from his belief in the fundamental importance of hystricognathy in rodent classification and a return to the acceptance of the basic importance of hystricomorphy (see below, p. 513).

Were caviomorphs the descendants of one or two successful middle Eocene raftings of African thryonomyoids to South America, one would hardly expect that, by early Oligocene time, they would have become more diversified, more numerous, and in a number of cases more specialized than their contemporary African relatives, the descendants of the stock from which they supposedly came.

The Composition of the Deseadan and Fayum Rodent Faunas

Twenty-four species of Deseadan rodents, not all formally described, representing perhaps 16 genera, have been recorded to date (Table 8). They are assignable to at least 7 families, and thus are almost as diverse as their North American contemporaries. Rodents form large percentages of the total mammalian assemblages in the better known local faunas. As noted in the Introduction (p. 374), each of these contains one rodent species that outnumbers all the rest, one

TABLE 8. RODENTS REPORTED FROM VARIOUS DESEADAN LOCALITIES.

	Patagonia				Bolivia	
	Rinconado de los Lopez	La Flecha	Cabeza Blanca	Laguna de los Machos	Salla	Lacayani
Platypittamys brachyodon	2					
Migraveramus beatus					1	
Sallamys pascuali					12	
Xylechimys obliquus				1		
Deseadomys arambourgi		1	1			
Deseadomys loomisi			1			
Scotamys antiquus		ca. 45	1			
Scotamys sp.						*
Cephalomys arcidens		12	100+			
Cephalomys plexus		1	32+			
Cephalomys sp.			1			
Cephalomys bolivianus					1	
Litodontomys chubutensis			1			
Incamys bolivianus			1		79+	
Dasyproctidae aff. *Neoreomys*					1	
Branisamys luribayensis					19	
Asteromys punctus			1	1		
Asteromys sp.						*
Chubutomys simpsoni			1			
Eocardiidae indet.			2			*
Protosteiromys medianus		7	1			
Protosteiromys asmodeophilus		2				
Caviomorpha indet.		1	1			
Octodontoidea gen. et sp. nov. 1					?	
Octodontoidea gen. et sp. nov. 2					?	
Luribayomys masticator					1	
Number of species	1	7	13	2	8–9	3
Number of specimens	2	69	144+	2	115+	*

In addition, one specimen of *Palmiramys waltheri* from Uruguay.
* Species listed by Hartenberger, 1975. Number of specimens unknown.

or two others that are moderately abundant, with the remainder represented by one or two specimens; the predominant species is different in each local fauna. At any one Deseadan locality, so far as is known, only one fossiliferous zone is represented, in contrast to the Fayum situation (see below, p. 464).

Professor E. E. Williams informed us that he had encountered rather comparable conditions in collecting Neotropical reptiles. We therefore looked for data on numbers of Recent Neotropical rodents at specific localities. These were found in the records of a plague survey carried out in northeastern Brazil from 1952–55 by the then Serviço Nacional de Peste (now Superintendência da Campanhas de Saúde Pública), in the course of which nearly 40,000 specimens of rodents were collected. Ectoparasites obtained have been published upon (Guimarães, 1972 and references therein), but almost nothing, other than the essential preliminary task of identification (by Moojen), has been done on the hosts. Arcoverde de Freitas (1957, Table 1) has given the grand totals of the forms collected in the Noreste (an unofficial name, comparable to Patagonia or New En-

TABLE 9. RODENTS COLLECTED DURING THE PLAGUE SURVEY OF 1952–55 IN NORTHEASTERN BRAZIL (EXCLUDING STATE OF BAHIA).

Zygodontomys lasiurus pixuna	13,486	*Echimys dasythrix lamarum*	133
Oryzomys subflavus	7056	*Oryzomys lamia*	59
Cercomys cunicularius	5700	*Calomys* sp.	50
Wiedomys pyrrhorhinos	2643	*Calomys laucha tener*	36
Akodon a. arviculoides	2213	*Oryzomys* sp.	18
Galea spixii wellsi	2137	*Proechimys guyannensis arescens*	16
Oryzomys nigripes	1944	*Dasyprocta prymnolopha*	12
Holochilus b. brasiliensis	967	*Coendou p. prehensilis*	11
Oxymycterus angularis	948	*Calomys callosus expulsus*	4
Kerodon rupestris	523	*Sciurus (Guerlinguetus)* sp.	4
Nectomys squamipes	493	*Oryzomys capito laticeps*	2
Rhipidimys masticalis cearanus	439	*Echimys* sp.	1
		Total	38,990

Data from Arcoverde de Freitas, 1957, Table 1.

gland, bestowed upon the northeastern coastal states from Maranhao to Sergipe; Bahia is not part of the Noreste), and the subtotals by Distritos, large areas that cover three to thirteen Municipios (counties). His grand totals are given in Table 9. Seventeen genera, over a third of the total recorded in the entire country (Viera, 1955) and 24 species, are represented in this comparatively small and, for the most part, far from lush part of Brazil. It is interesting to note that the 7 commonest species make up 90% of the whole, and that each of 12 species constitutes less than 1%. Arcoverde de Freitas' breakdown shows, furthermore, that relative abundance may vary widely from one Distrito to another.

A Distrito, however, is too large an area for the kind of comparison needed. For this, the lists of parasitized specimens sent by the Serviço to Dr. Guimarães have been utilized, and from them the data presented in Table 10 have been compiled. The localities (Fig. 28) have been chosen with an eye both to geographic proximity or spacing, and to the sampling of different environments. Three of the localities, G, H, and I, are single collecting stations; the rest are the combined totals for collecting stations within a Municipio.

These environments may be briefly defined (Dr. P. E. Vanzolini, personal communication) as follows:

Caatinga: rainfall 300–800 mm per annum, vegetation highly xerophytic with Cactaceae very conspicuous, soils very shallow; a harsh environment.

Agreste: rainfall 1000–1100 mm, vegetation xerophytic but Cactaceae less conspicuous, soils somewhat better; a mitigated Caatinga.

Brejo: an island of forest within Caatinga or Agreste resulting from higher elevation and increased, although locally variable, rainfall; vegetation not summer deciduous.

Atlantic Forest: rain forest with highly variable rainfall, 1200–4000 mm.

Table 10 shows that not only is the predominant species frequently different but also that relative abundances vary widely from locality to locality, even between those in close proximity, e.g., H and I (Fig. 28), or in similar general environments, e.g., E and G. Two forms, *Oryzomys subflavus* and *Zygodontomys lasiurus pixuna,* are well represented at most localities, while almost half (11 out of 23) of the species occur at only one locality. In some cases, such as B and I, two species are about equally predominant numerically. As a rule, however, one species is predominant, although not in all instances (as at A and D) overwhelm-

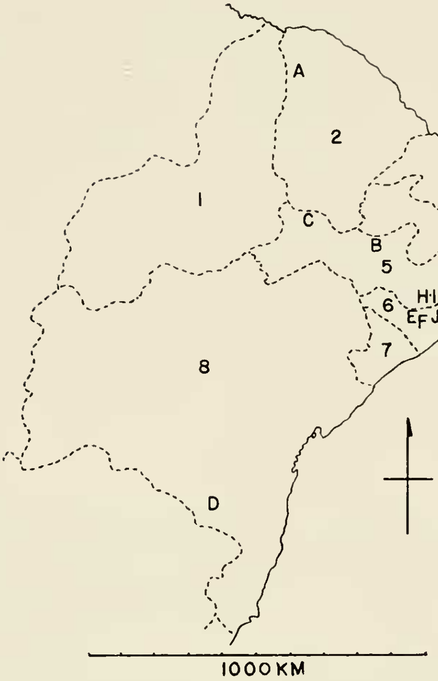

Figure 28. Map of northeast Brazil showing localities where rodents listed in Table 10 were collected (modified from Guimarães, 1972: Map 1). A–J: Collection localities listed in Table 10. States: 1—Piauhy; 2—Ceará; 3—Rio Grande del Norte; 4—Parahyba; 5—Pernambuco; 6—Alagoas; 7—Sergipe; 8—Bahia. Scale as shown.

ingly so. The situation at C, where *Cercomys cunicularius* is so remarkably numerous, might lead to the suspicion that a ratada, or population irruption, had been tapped by the collectors. This does not appear to be the case, since the records show peaks of abundance following the rainy season during each of the years 1952–54, which is not the classical ratada pattern. *Cercomys cunicularius* is an inhabitant of rocky places. Presumably locality C is such an area.

A general resemblance to the relative abundances encountered in Deseadan local faunas is apparent. The frequency distributions of La Flecha and Salla resemble those of localities E and G rather closely, and Cabeza Blanca shows some similarity to F. A collecting station for living forms, or a group of such stations, is of course not quite the same thing as an area in which sediments and skeletal remains are deposited. Sustained trapping will in time reveal the presence of even the rarest species and provide accurate estimates of relative abundance. The vicissitudes of taphonomy attendant upon the accumulation of a fossil assemblage, coupled with the accidents of collecting, can hardly be expected to yield precisely comparable results. Allowing for this, however, we believe that relative abundances of rodents at Deseadan localities were much like those now obtaining in Brazil (cf. Tables 8 and 10).

Deseadan caviomorphs were a rather diversified lot, ranging in size from small to fairly large (for rodents) and in crown height from brachyodont to hypselodont. Given the large numbers of the predominant forms—*Cephalomys* is the commonest Patagonian Deseadan mammal,

TABLE 10. RODENTS COLLECTED AT VARIOUS LOCALITIES IN NORTHEASTERN BRAZIL.

	A	B	C	D	E	F	G	H	I	J	Totals
Cercomys cunicularius[1]	4	413	1424	1	33	1				2	1878
Oryzomys subflavus	95	460		86	245	101	43	31	22	262	1345
Zygodontomys lasiurus pixuna	144	162		32	82	6	33	5	59	121	644
Akodon a. arviculoides	1						173	80	12	12	278
Oryzomys nigripes	19	12		51	3	36	11	14	67	17	230
Oxymycterus angularis	32	1			1		19	12		91	156
Holochilus b. brasiliensis	32		1		7	4	1		1	69	115
Calomys sp.				112							112
Rhipidomys masticalis cearanus	100	2					9				111
Galea spixii wellsi		13	56		2	6			1	2	80
Nectomys squamipes										39	39
Oryzomys lamia	20										20
Proechimys iheringi denigratus				19							19
Calomys laucha tener	5			13							18
Proechimys guyannensis arescens	15										15
Kerodon rupestris[2]	2	9	4								15
Wiedomys pyrrhorhinos	3	1		5					2		11
Proechimys a. albispinus				9							9
Coendou p. prehensilis	7										7
Echimys armatus	4										4
Calomys callosus expulsus				2							2
Oryzomys capito laticeps										1	1
Dasyprocta prymnolopha	1										1
Total											5110

Localities, here and on Fig. 28, are: A. Ceará, Municipio de São Benedito, Brejo; B. Pernambuco, Municipio de Triunfo, Brejo; C. Pernambuco, Municipio de Bodocó, Caatinga; D. Bahia, Municipio de Vitoria da Conquista, transitional between Caatinga and Atlantic Forest; E. Alagoas, Municipio de Palmeira dos Indios, Agreste; F. Alagoas, Municipio de Limoeiro de Anadia, Agreste; G. Pernambuco, Municipio de Caruaru, Fazenda Caruaru, Agreste; H. Pernambuco, Municipio de Garanhuns, Sitio Barrocão 3°, Atlantic Forest with areas of Agreste; I. Pernambuco, Municipio de Garanhuns, Fazenda Cristovão, Atlantic Forest with areas of Agreste; J. Alagoas, Municipio de Viçosa, Atlantic Forest.

[1] *C. c. inermis* at D; *C. c. laurentius* at the other localities.

[2] An inhabitant of rocky places, this species is perhaps under-represented.

Rattus and *Mus*, some of which were taken, have been excluded.

Determinations by J. Moojen. Certain nomenclatural emendations were made by B.P.

Incamys apparently the commonest Bolivian one—we suspect that by early Oligocene time the caviomorphs were well on the way toward achieving the numerical position and ecological diversity in the South American mammalian fauna that is held by rodents today. In the rich Santacruzian fauna of early Miocene age (21.7–18.5 m.y.b.p.; Marshall *et al.*, 1977) there are only 19 genera of rodents. Scott (1905), largely following Ameghino, a splitter of the first order, listed nearly 70 species, surely too high a number. Revision at the specific level has yet to be done. Data sufficient for any attempts at numerical analyses of the fauna are not available in the literature.

The Fayum thryonomyoids present quite a different picture. Three levels in the Jebel el Qatrani Formation yield mammalian remains: the lower fossil wood zone, the Yale Quarry G level, and the upper fossil wood zone; the lower and middle horizons are separated by an interval of 140 feet, the middle and upper by one of 150 feet (Simons, 1968: 21). The time involved in the deposition of these deposits apparently spanned most of the Oligocene (Simons, 1968: 4).

The rodents from this sequence com-

TABLE 11. THE FAYUM RODENT FAUNAS.

	Lower fossil wood zone (Quarries A, B, E)	Quarry G	Upper fossil wood zone (Quarry I)
Phiomys andrewsi	30	2	
Phiomys lavocati	9		
Phiomys paraphiomyoides		6	
Phiomys aff. *paraphiomyoides*			4
Phiomys or *Metaphiomys* sp.	2	6+	
Metaphiomys schaubi	6	59	
Metaphiomys beadnelli			2
Cf. *Metaphiomys* sp.	1		1
Phiocricetomys minutus			1
Gaudeamus aegyptius	11		
Neosciuromys simonsi			1
Unidentified		113+	9
Number of species	6	4	5
Number of specimens	59	186+	18

Data essentially from Wood (1968). The unidentified specimens have been recorded by Conroy (1976: 20) for Quarry I and by Simons (personal communication) for Quarry G; all were collected since 1968. Since this table was prepared, a collection in the MCZ of about 120 isolated cheek teeth and 1 lower jaw fragment, sorted from matrix from Quarry G, has become available. The jaw and 53 cheek teeth are referable to *Phiomys*, the remainder to *Metaphiomys*.

prise 8 to 11 species (3 possibly distinct forms were not named) representing 5 genera (Table 11) and 3 families. Wood (1968) placed all forms in one family, the Phiomyidae, a step justified on the basis of their morphological similarity. Lavocat (1973: 20), in agreement, pointed out that familial separation is only made possible by better knowledge of their Miocene descendants. We have previously stated (1959: 389) that Deseadan caviomorphs formed a relatively homogeneous group. This they did, but they were very much more diversified morphologically than their Fayum contemporaries. The much greater homogeneity of the Fayum than of the Deseadan rodents, and the fact that they were, individually, of smaller size, makes it difficult to understand the statement by Lavocat (1969: 1497) that the South Atlantic "a joué un rôle de filtre important, la faune de Rongeurs qui a réussi à passer en Amérique du Sud étant beaucoup moins variée que la faune autochthone d'Afrique, et constituée semble-t-il essentiellement par de petites formes arboricoles."

Table 12 compares the numbers of mammalian species collected by Loomis' expedition to Cabeza Blanca, Patagonia, with the numbers collected in one quarry (Quarry I) in the upper fossil wood zone of the Fayum during several field seasons. The difference between the two in the percentage of rodents is striking. At neither locality are the sediments uniform, and as regards the total number of specimens collected the two are not very different. Cabeza Blanca is a small hill, about 240 m long and averaging about 60 m in width, capped over much of its extent by the Miocene Monte Leon ("Patagonian") Formation; the Deseadan sediments there are 12.7 m thick (Loomis, 1914: 6, 21). Quarry I measures roughly 100 by 50 m and the sediments are about 1 m thick (E. L. Simons, personal communication). All matrix in Quarry I was meticulously examined, whereas no quarrying was carried out at Cabeza Blanca, all specimens collected having been found on the surface or in the process of weathering out. To compare the two seems fair, and it is clear that rodents

TABLE 12. COMPARISON OF PATAGONIAN AND FAYUM LOCAL FAUNAS.

Cabeza Blanca			Jebel el Qatrani, Quarry I		
	N	%		N	%
Notoungulata	125	44.3	Artiodactyla	147	38.3
Rodentia	102	36.1	Primates	105	27.2
Edentata	23	8.5	Hyracoidea	72	18.6
Litopterna	15	5.3	Creodonta	22	5.2
Marsupialia	11	3.9	Rodentia	18	4.7
Astrapotheria	6	2.1	Proboscidea	8	2.1
Condylarthra	1	0.4	Chiroptera	6	1.1
			Insectivora *s.l.*	3	0.8
			Sirenia	3	0.8
			Embrithopoda	2	0.5
Total	283		Total	386	

Numerical data for Cabeza Blanca from Loomis (1914: 19–20, 216); for Quarry I from Conroy (1976: 20, 22). All specimens identifiable to order—cranial, postcranial and dental—are counted. Of the Cabeza Blanca notoungulates, 31 (24% of the members of that order) are comparatively small, rather rodent-like members of the suborders Typotheria and Hegetotheria.

really are far less abundant at Quarry I than at Cabeza Blanca; it may be added that five other Yale quarries in the upper fossil wood zone contained no rodent remains at all. Had the large forms, arsinoitheres and gomphotheres, been better represented in Quarry I, the percentage of rodents would have been still lower. The Cabeza Blanca faunule is more nearly a representative sample of the ambient mammalian fauna; in Loomis' collection the smaller mammals constitute about 59% of the whole, medium-sized ones about 16%, and large ones 25%.

As regards the other Fayum levels, the lower fossil wood zone has yielded 59 specimens of rodents. This is the longest worked of the Jebel el Qatrani horizons, and Professor Simons is willing (personal communication) to estimate that about 2000 specimens of mammals have been collected from it. Taking this estimate, rodents constitute roughly 3% of the whole, despite the concentration of the Yale parties on finding the smaller faunal elements, which resulted in their increasing the number of known rodent specimens from the zone nearly fivefold.

In the middle Jebel el Qatrani, at Quarry G, the fossiliferous bed is homogeneous, 14 m long, 1 m wide and 4 cm thick at the center, tapering to feather edges at the sides, evidently what remained of the bed of a small stream. Except for one tooth of *Moeritherium* and one of an anthracotherid, the mammals are all small (E. L. Simons, personal communication). Here, rodents constitute about 58%, primates 27%, hyracoids 10%, creodonts 3% and "insectivores," *s.l.*, 1% of the total. The stream evidently ran through or near a habitat congenial to *Metaphiomys schaubi*, by far the commonest species in the deposit. Apart from a maxillary fragment of *Phiomys paraphiomyoides* found about a meter above the quarry, no other fossils were found near Quarry G (G. Meyer, personal communication). Quarry G is obviously a special case.

The available data indicate quite clearly that the rodents of the Jebel el Qatrani were on the whole less numerous relative to their contemporaries than were those of the Deseadan.

Passing on to taxonomic diversity, there is a paucity of rodent species in each of the three levels—6 in the lower fossil wood zone, 4 in Quarry G, and 5 in the upper fossil wood zone, compared with 13 recorded from one level at Cabeza Blanca. The difference in total taxonomic diversity is striking—7 families, perhaps 16 genera and 24 species in the Deseadan as against 3 families, 5 genera and 8 to 11 species in the Fayum, a point touched on by Hartenberger (1975: 429). This indicates to us that caviomorphs had been evolving considerably longer in South America than had thryonomyoids in Africa.

The Fayum and Deseadan rodent faunas are far apart as regards structural diversity. All Fayum rodents are small, except *Neosciuromys* ("*Paraphiomys*") *simonsi* (see below, p. 520), which was only as large as *Ondatra* or *Cynomys*. The Fayum rodents, in their entirety, are more specialized than any Oligocene rodents from any other part of the world in their marked degree of retention of dm_4^4, a character not met with in any known Deseadan rodent (this and other dental differences are discussed at length below, pp. 491–503). On the other hand, the Fayum thryonomyoids are far behind many Deseadan caviomorphs in cheek-tooth height. Nearly all of them are brachyodont, only *Neosciuromys* and *Gaudeamus* being incipiently mesodont. In the Deseadan, *Protosteiromys* is brachyodont; *Platypittamys* and *Migraveramus* are essentially brachyodont; *Sallamys* and *Branisamys* are brachyodont with incipient unilateral hypsodonty; *Deseadomys*, *Xylechimys* and *Asteromys* are mesodont, the first with some unilateral hypsodonty in the uppers (the other two are known only from parts of mandibular rami); *Cephalomys* and *Incamys* show marked unilateral hypsodonty, especially in the uppers; *Litodontomys* and *Chubutomys* (both known only from parts of mandibular rami) are hypsodont; and *Scotamys* is hypselodont. In cheek-tooth structure the Deseadan caviomorphs are much more varied than the Fayum thryonomyoids, and several of them are considerably larger. All this likewise suggests that caviomorphs had been resident in South America longer than had thryonomyoids in Africa.

There is one outstanding fact concerning the Fayum faunas: of all the rodents in the Yale and other museum collections, not one is attributable to any group other than the Thryonomyoidea. Lavocat (1973: 196, 252) reported that Simons had shown him an ulnar fragment from the upper levels of the Jebel el Qatrani Formation that was unquestionably that of an anomalurid. Search of the Yale collections has uncovered no trace of such a fragment. Simons informs us (personal communication to B.P.) that he has no recollection of ever having seen such a specimen, of ever having shown it to Lavocat, or of having Lavocat tell him that it was an anomalurid. Lavocat (1978: 80) stated, of anomalurids, that "their Oligocene record is extremely poor except for the Fayum ulna." This statement suggests that there is more basis for assuming that there were Oligocene anomalurids in Africa than is supported by the evidence, since the Oligocene record of anomalurids (except for the supposed Fayum ulna) is nonexistent.

If we contrast the Fayum assemblage with that present in one North American early Oligocene local fauna, the Porvenir Local Fauna in the Chambers Tuff Formation of southwestern Texas, we note that the latter includes 6 families of rodents, one represented by 3 and two others by 2 subfamilies; perhaps 13 genera; and some 15 species—and all this diversity is revealed by a total of only 44 specimens (Wood, 1974a: Table 1). To us it is inconceivable that, if primitive rodents had made a landfall on Africa in latest Paleocene or earliest Eocene, as proposed by Lavocat (1973: 166), so few rodent species, all of them members of one closely knit group, would occur in three levels of a formation laid down, during most of the Oligocene, at least 16 m.y. after such a landfall. Rodents do not evolve so slowly, especially in the com-

TABLE 13. RODENTS FROM THE EARLY MIOCENE OF EAST AFRICA.

Old natives (Thryonomyoidea)		Recent immigrants (all others)	
Diamantomys luederitzi	2180 + abundant at 3 levels of Napak	*Paranomalurus soniae*	70
		Bathyergoides neotertiarius	62 + "4 boites"
		Afrocricetodon s. songhori	65
		Megapedetes pentadactylus	53 + incisor fragments
Paraphiomys pigotti	1734		
Paraphiomys s. stromeri	110	*Paranomalurus bishopi*	51
Simonimys genovefae	46	*Vulcanisciurus africanus*	32
Phiomys cf. *andrewsi*	23	*Notocricetodon petteri*	21
Paraphiomys stromeri hopwoodi	20	*Paranomalurus walkeri*	20
Myophiomys arambourgi	19	*Proheliophobius leakeyi*	14
Epiphiomys coryndoni	14	*Protarsomys macinnesi*	9
Thryonomyoidea indet.	12	*Afrocricetodon songhori korui*	5
Kenyamys mariae	9	*Afrocricetodon* sp. 2	4
Elmerimys woodi	3	Sciuridae gen. et sp. indet.	3
Andrewsimys parvus	2	*Megapedetes* sp.	3
		Zenkerella wintoni	2
		Afrocricetodon sp. 1	1
Total counted specimens	4172	Total counted specimens	415
Percent of grand total	90.95%	Percent of grand total	9.05%
9 genera, 11 species or subspecies		10 genera, perhaps 16 species or subspecies	

Numbers based on the maximum figures given by Lavocat (1973). Specimens without precise locality, cited merely as "Kenya" are included, but those from Kirimun and "Lodwar" are excluded. The "4 boites" of *Bathyergoides neotertiarius* are of necessity not included.

plete absence of any competition. We must conclude, therefore, on the available evidence, that Lavocat's hypothesis of a very early date of arrival of rodents in Africa must be rejected.

To what extent the Fayum rodents were representative of the early Oligocene rodent fauna of the African continent is a question that must now be considered. Conditions prevailing during the deposition of the Jebel el Qatrani Formation—rivers, streams, lakes, ponds, forests and, possibly, savannah (Simons, 1968: 15–16)—would certainly seem to have been suited to the support of a rodent fauna at least as varied as that of Cabeza Blanca (cf. Tables 8 and 10), had such been in existence in Africa at the time.

Comparisons of the Fayum faunas with those of the late Burdigalian deposits of East Africa are instructive in this connection. Table 13 lists numbers of specimens of all East African rodent taxa, and the percentages that belong to the Thryonomyoidea and to the other rodent families and superfamilies that had, in the early Miocene, only recently invaded the African continent.

In the compilation of Tables 13 and 14 we have utilized the numbers of specimens enumerated by Lavocat (1973) under the taxonomic headings in the main body of his text, and those listed in his summary table on page 245 of that work. These two sources often disagree; in fact, they conflict over half the time. Most of the discrepancies are minor, but some are glaring. For example, 70 specimens of *Paraphiomys pigotti* and 48 of *Diamantomys luederitzi* from Rusinga are enumerated in the text (Lavocat, 1973: 22–23, 52), whereas 487 and 1647, respectively, are listed in the table; for *D. luederitzi*, 74 are enumerated from Songhor, but 1104 are listed in the table, although the text also specifies "nombreux autres échantillons" of upper teeth of *D. luederitzi* from Rusinga and Songhor (Lavocat, 1973: 52). Since specimens of upper

TABLE 14. NUMBERS, PERCENTAGES OF TOTAL RODENTS, AND NUMBERS OF TAXA OF RECENT IMMIGRANT RODENTS IN THE EARLY MIOCENE OF EAST AFRICA.

	Number of specimens	Percent of total rodents	Genera	Species & subspecies
Bathyergoidea	76 + "4 boites"	1.66	2	2
Anomaluridae	143	3.12	2	4
Pedetidae	56	1.22	1	2
Cricetidae	105	2.29	3	6
Sciuridae	35	0.76	2	2
Total	415	9.05	10	16

The "4 boites" of Bathyergoidea have of necessity been omitted from the calculations.

teeth of fossil rodents are usually distinctly rarer than those of the lowers, the fact that Lavocat lists only 28 specimens of lower teeth of this form from Songhor and 22 from Rusinga strongly suggests that the "nombreux autres échantillons" totalled significantly less than the 50 specimens of lower teeth. Lavocat's table (1973: 245) states that *Diamantomys luederitzi* is "Abondant" at three of the four levels of Napak, whereas, on page 52, he enumerates only 31 specimens from that locality. In the list of referred specimens of *Bathyergoides neotertiarius* (Lavocat, 1973: 110), there are included (in addition to 33 listed specimens) "4 boites" from Songhor, that we have perforce neglected in our calculations. Lavocat's table (1973: 245) merely lists this species as being "Abondant" at Songhor. In all cases of conflict we have used the higher of the numbers given by Lavocat. Even so, our Table 13 is clearly not complete. Lavocat enumerated, in his text, a total of 76+ rodent specimens from Napak, whereas Bishop (1967: 48) recorded 716 as having been collected there between 1958 and 1965. We must assume that these presumably unstudied specimens would not materially change the relative abundances shown by our Tables 13 and 14.

Numerically, the old natives (Thryonomyoidea) greatly outnumber the invaders (4172 to 415), the latter constituting only 9% of the total (Table 13). As regards taxonomic diversity, the invaders have an edge, 10 genera and 16 species or subspecies, as against 9 genera and 11 species or subspecies of thryonomyoids. This diversity results from the then-recent establishment of a land connection with Eurasia. In the early Miocene of East Africa we are witnessing the irruption of already differentiated southwest Asian faunal elements, that had not yet succeeded in dominating the autochthonous African rodent fauna. Lavocat (1973: 247) suspected that the invading cricetids had differentiated prior to their arrival in Africa; we go farther, suspecting that this was the case for all the non-thryonomyoid families, each of which was contributing an approximately equal amount to the total rodent fauna (Table 14). *Diamantomys luederitzi* and *Paraphiomys pigotti* constitute 85% of the total specimens; the eight commonest forms make up well over 90% (almost 95%), and the remainder, 17 in all, each contribute less than 1%.

Here in the early Miocene we see rodent faunas in full flower, as in the Deseadan of South America. The resemblance to the Recent faunas in the Brazilian Noreste (Tables 9, 10) is rather close, and the contrast to the Fayum rodent faunas is striking.

Lavocat (1973: 246), on the basis of differences in relative abundance of certain

TABLE 15. ORDINAL PERCENTAGES IN EARLY MIOCENE FAUNAS OF EAST AFRICA.

	Songhor	Koru	Mfwangano	Napak
Rodentia	82.5	86.5	68.6	64.0
Proboscidea	—	—	0.3	10.9
Artiodactyla	10.8	3.9	16.5	9.3
Primates	2.5	4.3	3.0	6.0
Others	4.1	5.3	11.6	9.8

Data from Bishop (1967: 48) for Napak (four levels lumped); from Bishop and Whyte (1962: 1286) for the other three. Cranial and dental specimens only.

rodent species, has tentatively suggested that the East African early Miocene fauna of Rusinga might be a little older than that of Songhor. As the Brazilian data show, this conclusion does not follow.

The early Miocene rodents of East Africa had achieved the numerical predominance (Table 15) characteristic of the order in areas where it has become well established, due primarily to the successful diversification of the thryonomyoids during the 10 m.y. of the Oligocene. That the Fayum thryonomyoids were far from having achieved such a position would seem evident (cf. Tables 12 and 15).

Under the circumstances, we are forced to conclude, for all the reasons discussed above, that the Fayum rodents were indeed representative of the early Oligocene rodent fauna of Africa.

The degree of diversity and numerical abundance attained by the Fayum thryonomyoids, whether placed in one family as was done by Wood (1968), in three closely related families as we do here, or in four as was done by Lavocat (1973: 160), was certainly no greater and probably less than that of the Recent Australian murids. These rodents belong to three subfamilies, the Murinae of Asian origin, the Hydromyinae and the Pseudomyinae. The Hydromyinae originated in New Guinea, the Pseudomyinae in Australia (Tate, 1951: 217–221), the two areas having been separated a significant portion of the later Tertiary. Intermigrations occurred during Pleistocene periods of low ocean levels. A single rodent incisor has been reported from the Pliocene Otibanda Formation of New Guinea, dated at 5.7–7.6 m.y.b.p. (Plane, 1967: 56). In Australia, the "Pseudomyinae differentiated, spreading into all the usual rodent niches, including burrowing (*Mastacomys*), saltatorial (*Notomys* and, partially, *Conilurus*) and arboreal (*Mesembriomys* and, partially, *Conilurus*), as well as the more typical scampering niche . . ." (Wood, in press, b).

Isolated pseudomyine molars have been reported from the Pliocene Chinchilla local fauna of southeastern Queensland, dating from about 4 m.y.b.p., and a single rodent incisor was found in the slightly older (4.5 m.y.b.p.) Bluff Downs Formation of northern Queensland (Archer and Bartholomai, 1978: 15–16), but no rodents are included in the extensive microfauna of the Hamilton Formation of Victoria, dated at 4.3 m.y.b.p., in spite of extensive sieving (Turnbull and Lundelius, 1970; Archer and Bartholomai, 1978: 15). This strongly suggests that the rodents had only just reached northern Australia in Bluff Downs time, and that their apparent absence from the Hamilton fauna represents a real absence from the southern border of the continent at that time (Archer and Bartholomai, 1978: 15; Turnbull, personal communication; Wood, in press b). The success of introduced rabbits in Australia should be a clue as to how rapidly rodents would have spread when they reached Australia (or the equally island continents of Eocene South America and Africa).

"That is, the present diversity of the Pseudomyinae represents the maximum differentiation that members of this rapidly reproducing and rapidly evolving order could achieve, in an area of continental size, with no real competition of any kind, in about 4.5 million years" (Wood, in press b).

The comparison of the diversification

of the Fayum thryonomyoids with that of the Australian pseudomyines strongly implies that rodents had been in Africa no more (and probably significantly less) than 4.5 m.y. before the deposition of the lower fossil wood zone. This would mean that rodents first reached Africa no earlier than late in the Eocene. The much greater diversity and abundance of the Deseadan caviomorphs is in accord with their having been in South America two or three times as long, probably having reached South America 10–12 m.y. before the Deseadan, presumably immediately after Musters time (Wood, in press b). Therefore, derivation of the Caviomorpha from the thryonomyoids would appear to us to be an untenable hypothesis.

As we have pointed out before (1959: 397, n. 32), if transatlantic rafting of rodents had occurred, on faunal grounds it would be more likely to have been from South America to Africa. Now as then, we do not take this possibility seriously. Platyrrhine primates also make their first appearance in the Deseadan, and it is not surprising that a nearly identical gamut of opinions regarding their dispersal has been run. Hoffstetter (e.g., 1972) has advocated rafting from Africa, while Szalay (1976: 426) has suggested rafting in the reverse direction. In answer, Hoffstetter (1977) cited the much greater abundance and diversity of the Fayum primate fauna as a telling argument against such a view. He is quite right—and precisely this same argument is equally valid evidence against the possibility of a rafting of thryonomyoids to South America. Relationships and place of origin of the platyrrhines are open and lively questions. Transatlantic rafting of the ancestral stock is perhaps a little less unlikely than rafting of ancestral caviomorphs (there is not so much evidence against it), and so cannot be ruled out entirely. Nevertheless, we adhere for the present (Wood, 1981) to the third and older alternative, that catarrhines and platyrrhines have descended from a common ancestral stock that lived in the southern parts of the northern hemisphere, and which reached Africa and South America independently. For further discussion of the difficulties involved in transatlantic rafting, see Simons (1976), who has informed us (personal communication) that in his opinion such resemblances as exist between the Deseadan primate *Branisella* and the Fayum primates are of a general nature and indicate no special affinities.

With that, we may proceed to a consideration of certain other items of evidence that have been cited to support a thryonomyoid ancestry for the caviomorphs.

The Evidence from Parasitic Nematodes

Hoffstetter (e.g., 1975: 522–523) and Lavocat (1973: 256) have indicated that evidence from certain parasitic nematodes favors an African origin for the Caviomorpha. Use of the data from these parasites is complicated by the complete absence of a fossil record to provide a time scale for nematode evolution, by the fact that there are probably very large gaps in our knowledge of present-day nematodes and their distribution, and by the fact that it is as difficult for paleontologists to interpret the data from parasites as for parasitologists to interpret those from fossils. Nevertheless, since nematodes have been cited to support thryonomyoid-caviomorph relationships, we have ventured into this gray area of interpretation, feeling that, at least, we can speak on the subject with as much authority as do Hoffstetter and Lavocat.

The nematode groups in question are the Heligmosomidae (Durette-Desset, 1971) and the Oxyurinae of the Family Oxyuridae (Quentin, 1973a, 1973b, 1973c).

Durette-Desset's concept of the Heligmosomidae would seem to be that of a grade rather than a clade, since she evidently believed (1971: Figs. 95–96) that the evolutionary "lignées" (all but one consisting of separate subfamilies) arose independently from different genera of the ancestral Family Trichostrongylidae, and developed their heligmosomid features as parallelisms. The major host group is the Rodentia, heligmosomids being reported in 17 of the living families.

Among Old World hystricognaths, *Thryonomys* is infected by *Heligmonella* (Heligmonellinae), the hystricids by *Heligmonella* and by *Paraheligmonina* (Brevistriatinae) in Africa and by *Cordicauda* (Brevistriatinae) in the Oriental Region, and the bathyergids by *Ortleppstrongylus* (Impalaiinae). There are no records for *Petromus*.

Within the caviomorphs, there is a sharp cleavage. Cuniculidae, Caviidae, Hydrochoeridae and Chinchillidae harbor *Vianella* (Vianniinae) whose other hosts are didelphids; presumably a transfer from the latter to the former was involved here. Echimyidae, Dasyproctidae and Erethizontidae are afflicted by members of the Subfamily Pudicinae, the echimyids by *Pudica*, *Heligmostrongylus* and *Pseudoheligmosomum* (Capromyinae, only, for the last), the dasyproctids by *Pudica* and *Heligmostrongylus*, and the erethizontids by *Heligmostrongylus*. In addition, *Paraheligmonella* (according to Durette-Desset, 1971: 50, the reference of this genus to the Heligmonellinae is questionable) has been recorded from the echimyids *Cercomys* and *Capromys*, and a species of *Stilestrongylus* (Nippostrongylinae), a genus otherwise confined to Neotropical cricetids, occurs in an echimyid, presumably another case of transfer. Heligmosomids have not been reported from the Octodontidae, Abrocomidae or Dinomyidae.

Durette-Desset doubted that host specificity is of primary importance in the Heligmosomidae, believing, rather, that diversification of the family came about mainly by various evolutionary "bursts" that accompanied expansion of suitable host groups. She postulated that heligmosomids were not in existence in the Paleocene (1971: Fig. 86), the various "lignées" having arisen during the Eocene. The "lignée" of interest in the present connection is that of *Heligmonella*. From the Subfamily Heligmonellinae there arose, in the late Eocene or early Oligocene according to Durette-Desset, the Pudicinae in South America and the Brevistriatinae in the Old World, and, in the later Tertiary, coinciding with the rise of the Muridae, the Nippostrongylinae. With the exception of *Paraheligmonella* in certain echimyids, the heligmonellines are Old World in distribution (Palaearctic talpids, Palaearctic and Oriental lagomorphs, and an Oriental sciurid in addition to *Thryonomys* and African hystricids).

However, Durette-Desset (1971: 50) apparently considered it uncertain as to whether *Paraheligmonella* was actually a heligmonelline. "Le fait que nous classions ce genre dans la même sous-famille qu'*Heligmonella* (mais en le considérant comme un peu plus évolué) implique une invasion de l'Amérique du Sud par les Rongeurs africains. Nous devons insister sur la fragilité de notre hypothèse, puisqu'elle ne repose que sur la structure du synloph. D'autres éléments, au contraire, sont déjà assez charactéristiques de la faune sud-américaine (division de la dorsale, arêtes discontinues)." It is this very, very tentative suggestion, that the subfamily crossed the South Atlantic inside rafted thryonomyoids, that Lavocat and Hoffstetter have emphasized.

Other interpretations would seem possible. In the first place, as we understand Durette-Desset's reservations, it seems entirely possible that her very tentative reference of *Paraheligmonella* to the Heligmonellinae may be incorrect, and that the features uniting *Paraheligmonella* and the Heligmonellinae evolved as parallelisms, an amount of parallelism apparently no greater than that which she accepts in the parallel evolution of the subfamilies from the ancestral Trichostrongylidae. If so, heligmosomid support for transatlantic rafting collapses at the outset. Secondly, we do not see that there is any basis for assuming that the heligmosomids were not in existence during the Paleocene, especially since didelphid marsupials and insectivores, two other groups parasitized by them, were then present, and remembering the lack of host specificity that Durette-Desset stresses. In discussing the relationships between heligmosomid evolution and rapid radiations of host groups, Durette-Desset has omitted the most important rodent evolutionary "burst" of all, the protrogomorph-franimorph radiation of latest Paleocene and early Eocene time. Rodents being the major host group (approximately 80% of the species listed by her infest members of this order), it seems unlikely to us that heligmosomids would not have profited from this radiation. We suggest, therefore, as an alternative possibility, that heligmonellines arose in Paleocene time in Holarctica, parasitized the ancestral hystricognath infraorder Franimorpha and their descendants, and subsequently gave rise to the Pudicinae in South America and to the Brevistriatinae in the Old World. *Paraheligmonella*, if correctly referred to the Heligmonellinae, would be, in this view, a surviving New World heligmonelline, not a transatlantic immigrant from the Old World.

In passing, it may be stressed that bathyergids are parasitized by members of the Subfamily Impalaiinae, which does not infest any other Old World hystricognaths. We believe that this was considered by Durette-Desset to be the most primitive of the "lignées"; she indicated that the subfamily originated in the middle Eocene (1971: 98), and in her phylogenetic chart (1971: Fig. 95) she shows this as the left hand "lignée." If Lavocat was correct (1973: 256) in his opinion that the distribution of nematodes is a key to host interrelationships, we feel that these data should have given him pause in attempting to derive the Bathyergoidea from the Thryonomyoidea (1973: 150–153).

In the case of the Oxyurinae, the major host group is again the Rodentia; members of 13 families are at present known to be infested by oxyurines. Other hosts, so far as recorded, are: Marsupialia (Australia only), Dermoptera, Lemuroidea, Platyrrhini, Leporidae and selenodont Artiodactyla. This is a very mixed bag, which suggests that knowledge of the distribution of the subfamily may be far from complete. No oxyurines have so far been recorded for either *Thryonomys* or *Petromus*. Four genera—*Hilgertia*, *Heteromyoxyuris*, *Helminthoxys* and *Evaginuris*—are of interest in the present connection.

Hilgertia, which is not very closely related to the others (Quentin, 1973c: Figs. 21, 23–24), is known from *Ctenodactylus* and *Heterocephalus*. Ctenodactylids were certainly of Asian origin (Wood, 1977a) and we believe bathyergids were, as well (see below, p. 516).

The other three genera, which form a closely related group, are, with the possible exception of two species of one of them, New World forms. *Heteromyoxyuris* infests heteromyids, a North American family which does not, as Quentin stated (1973c: 1092), date from the early Eocene but from the early Oligocene.

The various species of *Helminthoxys* are divided by Quentin (1973c: 1081) into four "lots." The first of these infests *Lagidium*, the second *Capromys*, the third *Microcavia* ("*Caviella*"), and the fourth *Dasyprocta* and *Cercomys*. Relying on our diagram (1959: Fig. 34) of caviomorph relationships that hypothesized early Miocene dates of origin for the Caviidae and the Capromyidae (in which, following a consensus, we then included the myocastorines), Quentin suggested (1973c: 1092) that infestation of these by two of the principal "lots" of *Helminthoxys* "indiquerait effectivement une évolution plus récente de ce genre." This may have been the case, but we know of no reason why the caviids could not have inherited these parasites from the extinct, broadly ancestral Eocardiidae. The Capromyinae, as we now restrict them (p. 393), are unknown prior to the Antillean late Quaternary. The other two families harboring species of this genus, like the Eocardiidae, go back to the Deseadan, so there seems to be no reason why *Helminthoxys* could not date at least from the early Oligocene.

Species of *Evaginuris* have been recorded, in the New World, from *Erethizon, Coendou,* and *Dinomys.* The type species, the North American *Evanginuris compar,* has been found in the domestic cat (the source of the type material) and in *Odocoileus,* as well as in *Erethizon dorsatum* and *E. epixanthum.* With this distribution, one wonders where else the species may occur. Interest here, however, centers on the two Old World reports of species of this genus.

Evaginuris evoluta (von Linstow) was originally—and summarily—described as a new species of *Oxyuris* (von Linstow, 1899: 20). When Quentin examined the type material, he found it to be "en mauvais état," "3 femelles desséchées, en fragments . . . . Ce matériel a pu être réhydraté en partie . . . par le procédé du phosphate monosodique" (1973c: 1068). How much of the original structure is recapturable by this technique is not for non-specialists to say. However, there is some uncertainty as to the provenance of these fragments, although Quentin (1973a: 2015) cited *E. evoluta* as "parasite d'un *Hystrix brachyura* originaire de Malaisie." Von Linstow, however, merely listed "*Hystrix brachyura* (?)*" without further details, although for other species of nematodes that he described in the same paper he was meticulous in recording localities and collectors. He added, in the footnote: "*Manuscriptname, dessen Identität nicht mehr festzustellen ist." We are thus left with unanswered questions. Was von Linstow in doubt as to whether the manuscript name, i.e., the host datum, was correctly associated with the caecum in which he found the oxyurine specimens, or was it the identification of the host that he questioned? If the host datum was essentially correct, could the animal have been a zoo inmate, housed in a cage adjacent to that of, perhaps even shared with, some erethizontid?

A second species of *Evaginuris, E. stossichi* (also originally referred to *Oxyuris*), has been reported from *Hystrix cristata* (Quentin, 1973a: 2015). Again, there seem to be problems with this species, which was originally given a very incomplete description (Quentin, 1973b: 1403). In 1956 "Vuylsteke . . . identifie à nouveau l'espèce chez un *Hystrix cristata* du Jardin Zoologique d'Anvers . . ."; these specimens were studied by Quentin and were the basis for his transferral of the species to *Evaginuris.* Since this specimen of *Hystrix cristata* was definitely a zoo inmate, the question raised above about the source of the *Evaginuris evoluta* infestation is equally applicable here.

We cannot answer the questions we have raised, but it seems obvious to us that the records are somewhat suspect, and that they should be confirmed from field collected specimens before they can be accepted at face value.

Even should the records be confirmed, there would be no necessity to invoke transatlantic rafting to account for the occurrence of *Evaginuris* in New and Old World porcupines. Quentin believed that *Evaginuris* was descended from *Heteromyoxyuris* or something very similar. The presence of this last genus in the wholly American (and, in the Oligocene, exclusively North American) Heteromyidae argues strongly that members of this group of oxyurine genera were present in the North American Eocene. They could not have been parasites on the Heteromyidae, nonexistent at that time. Some extinct family or families of rodents were presumably involved. If these had a Holarctic distribution, *Heteromyoxyuris* and, very possibly, *Evaginuris*, also had a similar distribution, and could have independently transferred to Asian hystricid descendants of the ancestral rodent hosts, as well as to Middle America, where they would have been ready to migrate to South America with the ancestral caviomorphs. It seems to us that those who are not willing to accept this view must face the difficult paleobiogeographic problem of explaining how the ancestral *Evaginuris* was able to reach the Old World tropics after having evolved from the North American *Heteromyoxyuris*.

Furthermore, if it is proposed that the distribution of *Evaginuris* be considered a support for the hypothesis of the derivation of the Caviomorpha from the Thryonomyoidea, it seems most surprising to us that the Old World members of *Evaginuris* should be confined to hystricids, absent from Africa, so far as anyone knows, until late Tertiary, and be unknown in the thryonomyoids, the group some of whose members supposedly crossed the South Atlantic carrying *Evaginuris*.

In summary, the evidence from nematodes cited as favoring transatlantic rafting is shaky indeed, and the support it offers for an African origin of the Caviomorpha has been grossly exaggerated. Further, even if the evidence for close relationships of the nematodes of caviomorphs and Old World thryonomyoids were accepted as being as clear-cut as indicated by Hoffstetter (1975: 522–523) and Lavocat (1973: 256), the data are capable of other, at least equally plausible, interpretations.

Comparisons of Caviomorpha and Old World Hystricognathi

We may now pass to a consideration of the hystricognathous rodents themselves, investigating the resemblances between the New and Old World forms. The points of similarity are numerous, which of course accounts for the controversies that have raged about the degree of relationship. There are three questions. First, which of these similarities are confined to the Caviomorpha and the Old World hystricognaths, and which are found as well in one or more of a variety of sciurognathous rodents? Secondly, which features are found in the North American Eocene hystricognaths, and which are limited to the Oligocene and later caviomorphs and Old World hystricognaths? Thirdly, are the resemblances that are confined to the Oligocene and later hystricognaths of so overwhelming and so exclusive a nature as to demand direct descent of the caviomorphs from hypothetical middle Eocene African thryonomyoid ancestors, or could they be the results of independent descent from a common, northern hemisphere franimorph ancestry combined with parallel evolution occurring subsequent to geographic separation? We shall discuss the answers to the three questions together.

(1) *General*. Lavocat (1973: 168) has listed, without discussion, 16 "principal common characters" of the Old World hystricognaths (his Phiomorpha) and the Caviomorpha. We believe that he omitted discussion because he had recently covered some or all of these points in detail (Lavocat, 1971a), although he did not cite this paper in this connection. These characters—some of them emphasized as early as 1839 by Waterhouse—and others have been reviewed repeatedly (Alston, 1876; Winge, 1887; Tullberg, 1899; Landry, 1957; Lavocat, 1974b, 1976; Wood, 1974a, 1975a; Hoffstetter, 1975—to give only a partial list). We regret the necessity of again going over this ground.

Lavocat's 16 characters are discussed below, in a somewhat different order than that in which he listed them; the italicized statements heading each section are his identifications of the characters, in translation. We have added a few other characters that he did not mention. In the course of our comparisons we have examined approximately 1000 skulls representing nearly all Recent hystricognath genera, mostly from the Museum of Comparative Zoology.

Lavocat (1971a) went into some detail as to structural similarities between the caviomorphs and the Old World hystricognaths, which he felt were too great (*op. cit.*: 521) to have developed as parallelisms. He stated that the occurrence of the same features in sciurognathous forms does not prove relationship. This is the problem that faces the student of rodents—when are identical structures proof of close relationship, and when does identity merely indicate parallelism? We have tried to find data supporting or contradicting Lavocat's statements. The necessity of providing documentation for our disagreement with some of his conclusions has considerably lengthened this section of our paper.

(2) *Hystricognath mandible.* This is the basic character of the Suborder Hystricognathi, and the only feature known to us that is universally present in hystricognaths and never present in sciurognaths. Hoffstetter (1973: 159, 161) seemed willing to accept the multiple origin of hystricognathy, not believing that *Prolapsus* or *Tsaganomys* had anything to do with the Hystricognathi. He eliminated *Tsaganomys* from the Hystricognathi because it was not hystricomorphous, but apparently was willing to accept the equally non-hystricomorphous bathyergids as members of the Hystricognathi. It is possible that hystricognathy evolved more than once in the course of rodent evolution, but we believe that acceptance of such an occurrence would mean that there are no morphological features (and probably no non-morphological ones) that can be used in establishing subordinal divisions of the Order Rodentia, since all other structures have already been shown to have evolved independently, in various groups of rodents, by parallelism (Wood, 1975a: Fig. 1). Furthermore, if hystricognathy can be assumed to have developed more than once among rodents as parallelisms, we believe that there is no justification whatever for assuming special relationship between the Caviomorpha and the Old World hystricognaths. We prefer to accept, as a working hypothesis, the postulate that hystricognathy originated only once, in the late Paleocene, probably of North America, and that it began as the condition that Wood has variously referred to as "incipiently hystricognath" (1962a: 117, 122; 1974b: 31, 42–43; 1977b: 104; 1981: 81, 82), "hystricognath condition" (1962a: 142), or "subhystricognathous" (1975a: 79; 1981: 86), rather than springing into existence full-blown, like Athena (Wood, 1980c: 270). We therefore include in the suborder all forms that are subhystricognathous or hystricognathous, believing them to have been derived from late Paleocene franimorphs such as *Franimys*. Since some franimorphs were fully hystricognathous (Wood, 1972: Fig. 1; 1974b: Fig. 5), inheritance from a common ancestor is, at the very least, as plausible a hypothesis to explain the possession of such mandibles by the Caviomorpha and the Old World hystricognaths as is one postulating a direct thryonomyoid-caviomorph relationship.

One of the major changes that developed among rodents in general during the Eocene was the increase in gnawing ability. This involved a number of structural changes: the forward growth of parts of the masseter, increasing the length of that muscle for more efficient gnawing (Wood, 1965: 116–119; Lavocat, 1971a: 519); in some forms, the lengthening of the *M. pterygoideus internus*, which served the same function as the lengthening of the masseter; and the modification of the histology of the incisor enamel, increasing its strength (Wilson, 1972: 220–222). One very important point to note here is that these changes did not occur instantaneously as the result of a single mutation, but built up gradually over considerable periods of time. Nor were they universally correlated with each other, but rather each feature evolved independently. Any slight shift in any one of these features would have been selectively advantageous. All of these changes may be observed taking place among North American Eocene franimorphs.

We do not know whether the Caviomorpha, the Thryonomyoidea, the Bathyergoidea and the Hystricidae developed full hystricognathy independently from subhystricognathous franimorph ancestors, inherited it directly from hystricognathous franimorphs, or whether the Old World forms inherited it from a common ancestor later than their common ancestor with the caviomorphs. There is at present no way of choosing among these choices other than following one's personal preferences.

A mandibular feature, not mentioned by Lavocat, that very frequently accompanies hystricognathy, although neither universally nor exclusively, is a projection extending posteriorly behind and below the condyle. This, the post-condyloid process of Woods (1972: Fig. 1A), varies in degree of prominence from absent (or at least scarcely defined) in, e.g., bathyergids, *Octodon*, *Echimys* and *Trichys*, to large in, e.g., *Kannabateomys*, *Dasyprocta*, *Dinomys* and *Hydrochoerus*, among living forms. It is slightly to moderately developed in Santacruzian caviomorphs and large in the East African *Paraphiomys*, but small in *Petromus* and *Thryonomys*. *Platypittamys* possesses a very small post-condyloid process, *Incamys* one of moderate size. Within the Franimorpha, this area has so far been described only in two species of *Reithroparamys*. The process is lacking in *R. delicatissimus*, incipient in *R. huerfanensis* (Wood, 1962a: Figs. 41D, 46F).

The degree of prominence of the post-condyloid process—indeed its very existence—is dependent on the size, and hence importance in the chewing function, of two masticatory muscles. These are *M. masseter lateralis profundus, pars posterior*, deep division, whose fibers insert on the lateral surface of the ascending ramus and on the posterior margin of the post-condyloid process; and *M. pterygoideus externus*, which inserts below the condyle and on the medial face of the process (Woods, 1972: 127–128, 130–131). Dependence of the process on the muscles is neatly demonstrated by *Ctenomys*, "in which the pterygoideus externus is somewhat small, the expansion has moved laterally and exists as a tubercle" (Woods, 1972: 131) below and lateral to the condyle (Ellerman, 1940: Fig. 38) for insertion of the deep division of the *M. masseter lateralis*. The very frequent association of the process with hystricognathy is, we suspect, because the development of the process has permitted the anteroposterior lengthening of the *M. masseter lateralis profundus, pars posterior*, deep division, and of the *M. pterygoideus externus*, serving the same function as the similar lengthening of *M. pterygoideus internus*, that produced hystricognathy. We suspect that the process arose independently in the Old and New Worlds, although it is possibly present in some franimorphs other than *Reithroparamys huerfanensis*, and may or may not have been present in the numerous franimorphs in which this area has not been preserved.

Although not strictly relevant to the question at issue, another direct consequence of hystricognathy or sciurognathy deserves mention. This is the course taken by the lower incisor in those forms in which the tooth has lengthened posteriorly. Since the axis in the posterior portion of this tooth in rodents is aligned dorsolaterally, the elongating base in hystricognaths can only terminate beneath the condyle, which is situated above it. In those sciurognathous forms in which elongation occurs, the base of the incisor can only extend upward lateral to the condyle, which is situated medial to the axis. The result is that, depending on the extent of elongation achieved, the base forms a protuberance on the outer side of the ascending ramus, ranging from small and low to so large as to reach the level of the condyle.

(3) *Pterygoid fossa opens anteriorly into the orbitotemporal fossa.* The pterygoid fossa of hystricognaths is bounded by the alisphenoid laterally, the palatine ventrally, anteriorly, and medially, and by the pterygoid posterolaterally; degrees of participation of these elements are highly variable, as are the size and shape of the fossa. "The main trends . . . are toward elongation of the internal pterygoid and horizontal positioning of the muscle. These trends [result from] the movement of the origin of the muscle deep into the pterygoid fossa, and the movement of the insertion to the tip of the extended and laterally displaced angle" (Woods, 1972: 131).

The opening into the orbito-temporal fossa is present in all Recent hystricognaths except *Hydrochoerus*, in which it has been secondarily blocked by the rearward extension of M^3. The opening is a feature much easier to detect in living than in fossil specimens. It is present in all early Miocene Santacruzian caviomorph skulls in which the area is adequately preserved; Scott (1905: 394) doubted its occurrence in *Neoreomys*, but we have found it to be present at the bottom of a deep and very narrow pterygoid fossa. An opening definitely occurs in the East African early Miocene *Paraphiomys pigotti* and *Bathyergoides neotertiarius* (Lavocat, 1973: Pl. 24, Figs. 3, 4; Pl. 7, Figs. 1, 5), and we assume one to have been present in other contemporary African hystricognaths, although Lavocat's figures do not show the opening in *Paraphiomys stromeri* (Lavocat, 1973: Pl. 24, Fig. 1) or *Diamantomys luederitzi* (Lavocat, 1973: Pl. 24, Fig. 2). The character is fully developed in *Tsaganomys*. The skull is not known for any Fayum thryonomyoid, but we suspect that their pterygoid fossa opened into the orbito-temporal fossa.

Among the few known Deseadan caviomorph skulls, only one specimen is sufficiently complete and adequately enough prepared to reveal details of the pterygoid region. This is PU no. 21945, *Incamys bolivianus* (p. 409). Here, connection with the orbit is definitely present. The character was probably present in all Deseadan caviomorphs.

In the three described early franimorph skulls, those of *Franimys, Reithroparamys* and *Protoptychus,* this area is either damaged or missing. Wahlert (1973: 8) remarked, of *Protoptychus*, that the fossa ". . . is very deep, and inadequately preserved for full description." The breakage in all of these skulls may have occurred because the area was weakened by perforation of the fossa, but there can be no certainty on this point at present.

With the opening of the dorsal side of the fossa, the origin of the *M. pterygoideus internus* passes forward mediad of a bridge of bone of varying length, the alisphenoid bridge of Woods (1972: 130). The bridge is formed in large part by the alisphenoid, dorsally, and to a much lesser extent by the pterygoid, ventrally. Woods reported the bridge as lacking in *Erethizon*. However, a large series of specimens in the MCZ reveals the bridge to be highly variable, ranging from present, but small and delicate, to interrupted in the center, to absent with no separate alisphenoid canal. Reduction is certainly secondary. A specimen of *Echinoprocta* shows a well-developed bridge and canal. Within a series of *Coendou*, variation extends from a well-developed bridge with a canal, to a delicate one without a canal.

The area of origin of *M. pterygoideus internus* extends forward to the vicinity of the sphenopalatine foramen, in various forms lying in a conspicuous channel in the adjacent bone. As the muscle enlarged, its passage encroached upon the alisphenoid canal. In some forms passage and canal are separated by a delicate bar of bone within the passage; in others a small projection remains to mark the former position of the separation; in yet others all trace of a division has been lost. In extreme cases, as in bathyergids, the origin of the muscle extends, via an opening, into the brain case as well. Where this occurs, the basisphenoid and the posterior portion of the presphenoid rise steeply to their dorsal midline, and form a narrow ridge flanked by depressions for the origin of the muscles.

Deepening and, ultimately, perforation of the fossa is a character definitely, although not exclusively, associated with hystricognathy. As is well known, it occurs elsewhere in the order among geomyoids and in *Spalax*; it is also present in *Aplodontia*, in which the perforation is large. Anterior to it and lateral to the sphenopalatine foramen in *Aplodontia* is a shallow but clearly defined channel as in various hystricognaths. We have not had the opportunity to dissect preserved material, but in a series of skulls we have detected dried muscle fibers within the passage and attaching to the channel leading forward from it, presumably indicating that it carried *M. pterygoideus internus*. The perforation in *Aplodontia* has usually been considered, as by Wahlert (1974b: 404), to be a very large alisphenoid canal. The internal maxillary artery and vein no doubt pass through together with the muscle, but, again as in various hystricognaths, no trace of a bony separation remains.

In all forms with a perforated pterygoid fossa, the angular region of the mandible, either the whole, as in hystricognaths, or the posterior part, as in the sciurognathous forms, is everted. The presence of a perforated pterygoid fossa in some sciurognaths adequately demonstrates, we believe, that this structure was capable of evolving independently, as parallelisms, among rodents. Furthermore, there is no evidence as to whether the perforation of the fossa arose among Eocene franimorphs, or not until the establishment of the modern infraorders.

We believe that hystricognathy began, in the early Reithroparamyidae, as a means of increasing the length of *M. pterygoideus internus*, because of its importance to the functioning of the lower incisors. At this stage, even very slight and incipient hystricognathy would have been of selective value and hence preserved. Selection for increasing incisor usage would have resulted in lengthening the internal pterygoid, which could have taken place either by moving the origin of the muscle (deepening the fossa), or moving its insertion (developing hystricognathy), or both. We believe that these two features (hystricognathy and deepening of the pterygoid fossa) evolved together, as secondary results of the muscle elongation (Lavocat, 1971a: 519; Woods, 1972: 131; Wood, 1980c: 269–270).

(4) *Inferior border of the zygomatic arch very often bearing an elevated vertical blade for the origin of the masseter.* What Lavocat refers to here, at least in part, is evidently the zygomatic masseteric fossa of Landry (1957: Fig. 11), the jugal fossa of Woods (1972: Fig. 1). This depression, when present, serves, together with the ventral margin of the posterior part of the malar, as the area of origin of *M. masseter lateralis profundus, pars posterior*, deep division (Woods, 1972: 127–128).

Among Eocene rodents, there is a well-developed jugal fossa in *Reithroparamys delicatissimus*, the only franimorph for which the zygomatic arch has been described (Wood, 1962a: Fig. 41C). A fossa is also present in *Paramys delicatus* and *P. copei* (Wood, 1962a: Figs. 2B, 13B), *Ischyrotomus horribilis* and *I. oweni* (*op. cit.*: Figs. 68C, 71C), and *Sciuravus nitidus* (Dawson, 1961: Pl. 5). The jugal fossa is poorly developed to nonexistent in *Thisbemys corrugatus* (Wood, 1962a: Fig. 36A), the only other Eocene rodent in which this area has been figured. It would thus seem that presence of a jugal fossa is a primitive rodent character.

In hystricognaths, the character is an extremely variable one. Among living Old World hystricognaths, the fossa is absent in the Bathyergidae and weakly, if at all, developed in the Hystricidae. Woods (1972: 127) stated that the fossa is absent in *Thryonomys* but present in *Petromus*, although no part of the muscle takes origin from it. We were unable to identify a jugal fossa in *Petromus*, but found that both genera have a more anteriorly situated depression in the lateral side of the zygomatic arch. This lies mainly in the maxilla, which in these forms extends farther back in the ventral portion of the arch than is generally the case in other hystricognaths (Ellerman, 1940: Figs. 26–27, 29–30). This anterior depression is larger in *Thryonomys*, but other than that we can detect no difference between the two forms, and consider both as lacking a jugal fossa in the strict sense. Lavocat (1973: 168) and Woods (1972: 127) apparently both equated the anterior depression of *Petromus* with the true jugal fossa, thus lumping two different bone-muscle relationships as one supposed character.

Among caviomorphs, the jugal fossa is absent or virtually so in the Erethizontidae, Chinchilloidea and Cavioidea, being essentially limited to the Octodontoidea. Even within this superfamily it varies from absent to large in the Octodontidae and from small to large in the Echimyidae.

The East African Miocene *Paraphiomys* and *Diamantomys* in general resemble *Petromus* and *Thryonomys*, with the exception that the more anterior (not the jugal) fossa presents more ventrally. Such Santacruzian erethizontid, cavioid and chinchillid specimens as are sufficiently well preserved to show this region lack the jugal fossa, as does the Deseadan cavioid *Incamys*. Of fossil octodontoids, the Santacruzian echimyid *Acarechimys minutus* (see Appendix 2) has a small fossa (Scott, 1905: Pl. 67, Fig. 10b) while the Deseadan octodontid *Platypittamys* shows no trace of one.

Since the jugal fossa serves as part of the area of origin of the deep division of *M. masseter lateralis, pars posterior*, and the post-condyloid process of the mandible as part of the area of its insertion, one might expect a fair degree of correlation between the two. This is definitely not the case, however. The process varies from small to large in those caviomorph superfamilies in which the fossa is essentially lacking, while within the Octodontoidea every change is rung from absence of both, to small size of one and large size of the other, to large size of both.

Presence of a jugal fossa is, therefore, not of any significance at higher taxonomic levels, and is, in any case, apparently a primitive rodent characteristic. The myological character associated with it, the high degree of differentiation of the deep from the superficial division of *M. masseter lateralis, pars posterior*, is significant. It occurs in all living hystricognaths that have been investigated in sufficient detail to reveal it. There is some evidence that the division of this muscle may be associated not only with hystricognathy, but also with hystricomorphy, since the hystricomorphous but sciurognathous ctenodactylids possess a well-defined jugal fossa. Whether or not this is accompanied by any marked degree of differentiation of the deep from the superficial division of *M. masseter lateralis, pars posterior*, apparently is not known.

These data indicate that the presence of a jugal fossa is not a hystricognath character; it could have been independently inherited from Eocene franimorph ancestors in those forms where it is present; or it could have been secondarily reacquired independently in the octodontoids and hystricids.

It should be pointed out that modification of the masseter complex began very early in rodent history, as indicated not only by the hystricomorphous franimorphs but also by the large jugal fossa borne on a descending flange, which extends over the entire length of the malar in the Bridgeran manitshine paramyid *Ischyrotomus horribilis* (Wood, 1962a: Fig. 68C).

(5) *In both, the infraorbital foramen is of the hystricomorphous type.* This is indeed a resemblance between the New and some of the Old World members of the suborder, involving, as it does, the same structural modifications and forward migration of the origin of *M. masseter medialis,* but it is not universal within the suborder—the protrogomorphous Tsaganomyidae and Bathyergidae (p. 517) lack it, and the foramen is very small for a hystricognath in *Platypittamys* (Wood, 1949: Fig. 2; 1974b: Fig. 3A). Nor, as is very well known, is this condition confined to the Hystricognathi. It occurs in the European Eocene to Oligocene Theridomyoidea; the Asian, African and European Ctenodactylidae; the African Anomaluridae and Pedetidae; the Eurasian, North American and African Dipodoidea; and the African glirid *Graphiurus*—all sciurognathous forms. *Protoptychus, Prolapsus* and, very possibly, *Rapamys* (Wood, 1962a: 148, Fig. 52A) show that hystricomorphy was early acquired by North American franimorphs. We suspect that it may have developed independently among Asian hystricognaths descended from protrogomorphous franimorphs, and that the fossorial bathyergoids are descended from franimorphs in which hystricomorphy had not become established. As has been demonstrated several times (Wood, 1974b: 38–41; 1975a: 75–77; 1977a: 133–136; 1981: 82), hystricomorphy evolved independently a considerable number of times—perhaps as many as ten or twelve—and cannot be considered proof of relationship, except insofar as parallelism indicates some relationship.

(6) *The malar heavy in front, with a sinuous suture with the maxillary.* Sinuosity of the suture does not necessarily accompany heaviness of the malar, and both features are extremely varied among the Hystricognathi. The bathyergids display neither. In hystricids, the suture varies from simple to slightly sinuous, and the malar may be either heavy (*Atherurus, Hystrix*), moderately heavy (*Thecurus*), or comparatively slender (*Trichys*). *Thryonomys* has a very heavy malar and a moderately to highly sinuous suture, *Petromus* one that is but little expanded with only a slightly sinuous suture. Among living caviomorphs, heaviness ranges from extreme (e.g., *Chaetomys*) to nonexistent (e.g., *Echimys*), and sinuosity of the suture, as, e.g., in *Dinomys, Myocastor* and *Spalacopus* (which has a slender malar) is the exception, not the rule.

The East African *Paraphiomys* (Lavocat, 1973: Figs. 2A, 3A) and *Diamantomys* (Lavocat, 1973: Fig. 4A,B) possess malars ranging from moderately slender, anteriorly, in *P. stromeri* and *P. pigotti,* to heavy, and the suture resembles that of *Petromus.* It is not preserved in any other described Oligocene or Miocene thryonomyoid.

The Santacruzian caviomorphs, like their living relatives, display variability as regards both features. Only in *Incamys* among early Oligocene hystricognaths is any part of this region preserved (Fig. 12), and here the suture, although irregular, could hardly be described as sinuous. The drawing of the skull of *Sallamys* given by Lavocat (1976: Fig. 1) shows the zygoma fairly well preserved, but with a straight suture. His stereophotograph (1976: Pl. 1, Fig. 4) seems to show about the same thing, except that only the dorsal and ventral roots of the zygoma are present. The only franimorph whose arch area is known is *Reithroparamys delicatissimus*, in which the malar is slender and the suture is not sinuous (Wood, 1962a: Fig. 41C). There is thus no evidence for (but only a little against) a sinuous suture in the early members of either the Caviomorpha or the Old World hystricognaths.

Among those rodents that are hystricomorphous sciurognaths, variation in anterior heaviness of the malar is also encountered, to an extent equal to that in hystricognaths. The heaviness ranges from nonexistent, as in anomalurids, through moderate, as in such zapodids as *Sicista*, to very great, as in *Pedetes*. This heaviness is almost never present in sciuromorphous or myomorphous rodents, *Castor* being a notable exception. It seems obvious to us that this is a character associated with evolving structural stresses, whose acquisition has been superimposed on a pre-existing hystricomorphous base. Sinuosity of the suture occurs in *Paramys delicatus* (Wood, 1962a: Fig. 2B), but not in other adequately known Eocene rodents.

Anterior heaviness of the malar and sinuosity of its anterior suture seem to us to be worthless as indications of caviomorph-thryonomyoid relationships.

(7) *Middle ear, malleus and incus of the same type. Malleus and incus fused.* The statement regarding the middle ear is apparently based largely on the investigations of Parent, whose work is available to us only in abstract form (Parent, 1976; Lavocat and Parent, 1971). Parent found that hystricognaths possess various middle ear characters in common, which is not surprising, and that thryonomyids, petromurids, hystricids and bathyergids can be distinguished from each other in this region, which is somewhat more surprising. Among the Caviomorpha, he recognized three groups: erethizontids (in which the subordinal characters are "peu marqués"), octodontoids, and cavioids plus chinchillids. Vucetich, however (1975: 486), found features of the middle ear that separate the Chinchillidae from the Cavioidea. Not surprisingly, parallelism crops up in middle ear structure. Certain hystricognath features are met with in *Anomalurus* and *Pedetes*, and *Agouti* ("*Cuniculus*") has a bulla that resembles that of the Hystricidae "de façon inattendue" (Parent, 1976: 244). We can see no evidence in this that caviomorphs were descended from any Old World group; in fact, the situation in erethizontids, as reported by Parent (1976: 244), can be interpreted as ruling out such a relationship. The degrees of differentiation seen within the Old and New World groups are what would be expected, given a rather distant common ancestry.

Knowledge of the middle ear cavity in hystricognaths does not extend farther back in time than the early Miocene (Lavocat, 1973, for *Paraphiomys*; Vucetich, 1975, for *Perimys*). The bulla is unknown in Fayum thryonomyoids, and its dissection has not been practicable in *Incamys*. Among the known Franimorpha, the tympanic is free of the skull only in the very early *Franimys*. Here, the ventral aspect of the periotic, although "difficult to interpret" (Wood, 1962a: 142) is in general similar to that of *Paramys*, as is to be expected. Comparison with most later forms, in which the tympanic surrounds the middle ear cavity, is difficult, being limited in large part to the promontorium. There is a decided difference in the size and shape of this latter structure between the primitive condition exhibited by the early Eocene forms and the more advanced one shown by the Miocene genera that lived some 30 m.y. later. An assessment of this difference must await some knowledge of intermediate stages, but we suspect that, under either hypothesis for the origin of the Caviomorpha, the common ancestors of the living caviomorphs and the Old World hystricognaths were not greatly advanced beyond the paramyid-reithroparamyid level.

Malleus and incus of the same type. As may be seen from the figures and descriptions given by Doran (1879: 413–419, Pl. 60), Tullberg (1899: Pl. 24), Cockerell *et al.* (1914: Figs. 117–119) and others, these ossicles are heavily built and more or less in line dorsally. The head of the malleus is large and elongate, varying from moderately (Bathyergidae) to extremely so (*Chinchilla*); the neck is short, and the lamina small.

Ossicles are frequently absent from within the bullae of fossil mammals. This is not surprising in view of field observations by one of us (B.P.) that fly larvae in the course of their development can pullulate through even the smallest openings in decomposing bodies and are fully capable of dislodging and moving out such small objects as ear ossicles.

Knowledge of the *ossicula auditus* of hystricognaths does not extend farther back than the Miocene. Among fossil hystricognaths only three examples of the malleus and incus have been reported: *Drytomomys aequatorialis* (Fig. 23A–C and Fields, 1957: 343, 347–349; Fig. 23E,F); *Perimys* sp. (Vucetich, 1975: 484, 488); and *Paraphiomys pigotti* (Lavocat, 1973: 34; Pl. 13, Fig. 4; Pl. 40, Fig. 1). All three sets, as might be expected, are of hystricognath type. *Drytomomys* is similar to *Dinomys*, but *Perimys*, a chinchilloid, is closer to *Cavia*, especially in the relative shortness of the head of the malleus, than to the living members of its superfamily. *Paraphiomys* seems to us to be close to *Petromus*; it is certainly very different from the bathyergids, and the head of the malleus is more slender than in *Thryonomys*. There is, as Lavocat noted (1973: 34), a resemblance to that of *Dasyprocta*.

In assessing the ossicular evidence, the same difficulty is encountered as in the case of middle ear structures, namely lack of information, in this case total, regarding pre-Miocene evolutionary stages.

Malleus and incus fused. Fusion of the malleus and incus is not confined to the Hystricognathi, since the Ctenodactylidae show it also, and Doran (1879) reported it as being variably present in *Dipus*. It would seem to be universally present in Old World hystricognaths. It is not a universal feature, however, among the Caviomorpha. Vucetich informs us (personal communication) that, in perhaps 1% of adult *Cavia* whose ossicles she has seen, she was able to separate the malleus and incus without breakage. We have recorded (1959: 292–293) a lack of fusion in some adult specimens of *Octodon*, *Aconaemys*, *Spalacopus* and *Echimys*; and such a lack had earlier been reported in *Proechimys* (Cockerell *et al.*, 1914: 372), and, earlier still, in *Myocastor* (Hyrtl, 1845). There is therefore no justification for the unqualified statement that fusion is universal in the Hystricognathi.

To the above list of non-fused ossicles, we now add a young adult of the late Miocene dinomyid *Drytomomys aequatorialis*. Fields' figures (1957: Fig. 23E,F), while suggesting fusion, showed a very definite groove between the bones. Subsequent to his work, the specimen was badly damaged with accompanying loss of the manubrium mallei and of the incus, the two ossicles parting at the groove. A thin film of matrix extended over the entire articular surface of the malleus separating it from the incus; fusion had not occurred (Fig. 29).

Lavocat reported that the malleus and incus of *Paraphiomys pigotti* were fused, presumably because they were lying within the bulla in an articulated position. His figure (1973: Pl. 13, Fig. 4) suggests that there is a matrix-filled groove at their junction. This raises the possibility that, as in the case of *Drytomomys*, they may have been separable in life. In fact, it would seem to us that, although lack of fusion can be demonstrated in fossil rodents if the ossicles are preserved separately, fusion can only be proven by serial sections or when a continuous groove between the ossicles is no longer present.

Vucetich (1975: 484), although not mentioning fusion, remarked of *Perimys* sp. that the suture between the two ossicles was simple on both sides.

In some, but not all, Old World hystricognaths the area of fusion extends to the

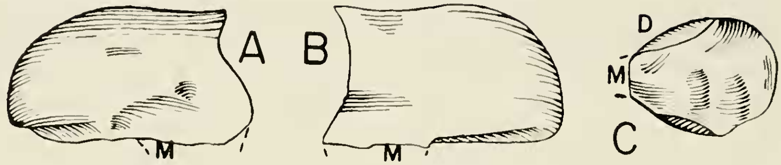

Figure 29. Malleus of *Drytomomys aequatorialis*, UCMP no. 41636, ×15. A. Dorsal view. B. Ventral view. C. Surface for articulation with the incus.

Abbreviations: D—dorsal side; M—broken manubrium.

crus longus of the incus, moderately so in *Thryonomys* (Tullberg, 1899: Pl. 24, Fig. 14; Wood and Patterson, 1959: 293, n. 4), although Doran's figure does not show this, and almost as far as the incudal articulation in bathyergids (Hyrtl, 1845; Doran, 1879: 413; Tullberg, 1899: Pl. 24, Figs. 1–2). *Hystrix* (Doran; Tullberg), *Petromus* (Tullberg and personal observation), and all caviomorphs for which ossicles are known display no such extension. We do not, of course, feel that the similar degree of fusion of the malleus with the crus longus of the incus indicates closer relationships of *Thryonomys* to the bathyergids than to *Petromus*.

Among those hystricognaths—and they constitute the great majority—in which fusion occurs, the time of onset of the fusion during ontogeny is variable. Available data are few but sufficient to demonstrate this. Doran has recorded fusion in newborn *Cavia*, "even in very young" *Dasyprocta*, and in "quite young" *Hystrix*, whereas in *Hydrochoerus* the ossicles are "often free in young" specimens; we have recorded fusion in juvenile *Thryonomys* and in adult, but not in juvenile, *Abrocoma*. Thus the available data suggest that the ontogenetic onset of fusion is earlier in Old World than in New World forms, and all stages from *in utero* fusion to complete lack of fusion may occur in the latter.

There has been no documented selective basis for the fusion of these ossicles. However, Dr. E. C. Oaks has suggested to us (*in lit.*) that it may be an adaptation against possible dislocation of unusually heavy ossicles such as characterize most of the Hystricognathi.

If the Caviomorpha were descended from rafted thryonomyoids, it seems most amazing to us that the more primitive condition (occasional absence of fusion) should be rather widespread among the Caviomorpha, presumably descended from a small founder population, and unknown in the Old World forms. We know of no basis for assuming that there has been a selective advantage for a neotenic retention of embryonic lack of fusion among the Caviomorpha that did not act on the Old World forms. Therefore, we conclude that the status of fusion of the malleus and incus supports one of two possibilities. Either the Old World hystricognaths were descended from caviomorph ancestors; or (much more probably, in our opinion), fusion was either incipiently present among the Franimorpha or was acquired independently, by parallelism, by the Old World and New World hystricognaths, as well as in such unrelated rodents as the sciurognathous ctenodactylids (Wood, 1975a: Fig. 1).

(8) *Similar arrangement of openings at the base of the skull.* We are not sure to what this refers, unless to the foramina for the cranial arteries. In view of the reported similarities in cephalic arterial circulation between the Caviomorpha and the Old World hystricognaths (Guthrie, 1963: 472; Bugge, 1971: 519–522; 1974a: 70–71; 1974b: 65–69), a similarity of the foramina through which the arteries pass is not surprising. Unfortunately, Old World Oligocene material (other than of

tsaganomyids) is unavailable to demonstrate either similarity or dissimilarity to the Deseadan caviomorphs.

Recent studies by Bugge (1971, 1974a, 1974b), Guthrie (1963) and Wahlert (1974a) have provided enough new information on the cranial circulation of rodents so that the arrangement of these blood vessels (or of the foramina presumed to have been occupied by them) can be used as an important adjunct to rodent classification. Bugge (1974a, 1974b) has developed a classification of the rodents, using the losses, during ontogeny, of arteries (especially the stapedial and internal carotid) from the primitive mammalian pattern. He reported (1974b: 78) that the "stapedial artery obliterates when the bulla and pars petrosa are nearly connected and when the chewing musculature is very strongly developed, and I think that there is some mechanical explanation for obliteration of the stapedial artery. But I do not know why the internal carotid artery is obliterated in some cases and not in others." It would seem possible that the same types of processes would have affected the internal carotid as the stapedial artery. If Bugge was correct, that the fusion of the bulla with the skull was responsible for the loss of the stapedial artery, this loss should have occurred among Eocene franimorphs, in some of which the bulla is fully developed and fused with the skull (Wood, 1962a: Fig. 41B,C; Wahlert, 1973: Fig. 2; 1974a: Fig. 5).

As pointed out by Bugge (1974a: 56, Fig. 15B), the arterial pattern of *Coendou prehensilis* is quite different from that of other hystricognaths; it is apparently most similar, among living rodents (other than *Erethizon*, in which, apparently, the cephalic arteries have not been studied, although a carotid canal was reported by Hill in 1935), to that of *Castor fiber* (Bugge, 1974a: Fig. 10C), and seems to be almost identical to what Bugge (1974a: Fig. 15D) described for *Oryctolagus* and *Lepus*. The difference between *Coendou* and the other hystricognaths is so striking that Bugge (1974a: 56) felt that the erection of a new Suborder Erethizontomorpha was needed (Bugge did not use the Suborders Sciurognathi and Hystricognathi that we are using; his suborders are therefore equivalent to our infraorders).

The cranial circulation of the Chinchillidae, Octodontoidea, *Thryonomys* and the Bathyergidae is essentially identical, with the internal carotid, proximal part of the stapedial and varying amounts of the central part of the supraorbital arteries having been lost (Bugge, 1974a: Figs. 14D, 15A). The Hystricidae differ by developing a transient anastomosis (a6) between the distal part of the internal carotid and the infraorbital arteries (Bugge, 1974a: Fig. 15C). Slightly different anastomoses occur in the cavioids, with a transient connection (a4) from the distal internal carotid to the supraorbital in *Dolichotis* (*op. cit.*: Fig. 14B); a transient one (a5″) from the same source to the infraorbital in *Cavia* (*op. cit.*: Fig. 14A); and a permanent connection in approximately the same area (a6) in *Galea* and *Dasyprocta* (*op. cit.*: Fig. 14C).

Problems arise in connection with reliance on the pattern of cranial circulation as a guide to rodent relationships. We do not know of the selective pressures that led to the changes, other than Bugge's suggestion that the loss of the stapedial artery was related to the fusion of the bulla with the skull. As a result, it is difficult to assess the weight to be given such changes. How can one be sure, in dealing with fossils, that an opening in the skull carried the blood vessels that one would anticipate, on the basis of the study of Recent forms? This point is raised by the observation by Wahlert (1974a: 373) that the carotid canal of *Marmota monax* carries the inferior petrosal sinus rather than the internal carotid artery, as is usually the case among rodents. Bugge (1974a: Fig. 11B) indicates the internal carotid artery to be absent in *Mar-*

mota marmota as well. Finally, how does one distinguish parallelism or convergence in the gain or loss of blood vessels from the inheritance of a pattern from a common ancestral source?

The similarities cited above between *Coendou*, *Castor*, and leporids, and the likewise great similarities between *Muscardinus* and *Aplodontia* (Bugge, 1974a: Fig. 13C,D), are certainly not indications of close relationships. The first three have interrupted the stapedial, supraorbital and internal ophthalmic arteries, and have acquired anastomoses a1, a2, and a3′ in the adult as well as a3 transiently during ontogeny (Bugge, 1974a: Figs. 10C; 15B,D). *Muscardinus* and *Aplodontia* have lost the internal carotid, stapedial and supraorbital arteries and have developed the a3 anastomosis; *Aplodontia* has also acquired an a3″ anastomosis. Since none of these forms are at all closely related, the losses and gains must be presumed to have occurred as convergent adaptations. If these similarities are not indicative of relationship, we see no real reason for believing that the similarly close resemblances between the chinchillids, octodontoids, *Thryonomys* and the bathyergids (Bugge, 1974a: Figs. 14D, 15A) could not either be inheritances from a common Eocene franimorph ancestry or the result of parallelism. The fact that three different types of anastomosis occur in the caviids (Bugge, 1974a: Fig. 14A–C) suggests that similarities and differences in the cephalic circulation need to be treated with caution.

The pattern of circulation described in *Coendou* by Bugge (1974a: 56) is certainly much more primitive than that in any other hystricognath that he dissected. As he has indicated (Bugge, 1974b: 78), "these arteries pass through canals in the cephalic bones and when these arteries are [lost, the] canals are also obliterated. Therefore I would think it most unlikely that such osseous canals should re-open for the internal carotid artery or the stapedial artery." If Lavocat is correct that all the caviomorphs (including the Erethizontidae) are descended from thryonomyoids, it is surprising that no trace of the internal carotid has been preserved in any of the Old World hystricognaths that Bugge dissected. However, and this we consider to be an important point, if the caviomorphs (including the Erethizontidae) *are* descended from thryonomyoids, it must follow either that the erethizontids have reacquired the internal carotid artery or that the loss of the internal carotid has occurred independently, as a parallelism, in the Old and New Worlds.

There is some evidence as to the situation in the fossils. Unfortunately, no cranial material is available from Oligocene thryonomyoids. Bugge (1974a: 63) thought that ". . . it is a reasonable assumption that both the internal carotid artery and the stapedial artery were already obliterated in the Oligocene-Miocene phiomyids . . . ." Lavocat (1973: 63), however, reported that, in *Diamantomys luederitzi*, "Le foramen carotidien s'ouvre en avant de la gouttière . . . qui se creuse entre la région postérieure du basi-occipital et la bulle. C'est un trou de toute la hauteur de la gouttière." As indicated above (p. 411), there is possibly a small carotid canal in *Incamys*. These observations suggest that the internal carotid artery was still present in *Diamantomys* and possibly in *Incamys*, again indicating that the artery has been lost independently in the New and Old Worlds. Incidentally, Wahlert (1974a: Fig. 10) identified a carotid canal in the North American early Oligocene franimorph cylindrodont *Ardynomys occidentalis*.

We feel, in summary, that the cranial circulation very probably indicates that the Caviomorpha and Old World hystricognaths are related, but that almost certainly one of their similarities, the loss of the internal carotid artery, occurred independently in the two hemispheres. How many of the other circulatory similarities are the result of parallelism and how many were inherited from common franimorph ancestors, we have no way of knowing at present.

(9) *Alisphenoid remaining in a low position.* This is an advanced character, not a primitive one as Lavocat's wording might suggest. In most Eocene rodents, as may be seen in the figures of Wood (1962a; 1974b: Fig. 4B) and Wahlert (1974b), the alisphenoid extends dorsally to or above the posterior root of the zygoma, to meet a descending portion of the parietal, the frontal and squamosal being separated. In nearly all later rodents, a reshuffling of relationships between these bones has taken place. The descending portion of the parietal was quickly lost and a squamoso-frontal contact was established, its extent largely depending on the degrees of reduction of the anterolateral portion of the parietal and of the dorsal portion of the alisphenoid. The latter may retain the size met with in the primitive rodents (e.g., *Aplodontia*, many sciurids, *Pedetes*) or may increase dorsally until it nearly (e.g., *Tamias, Pteromys*) or quite reaches the parietal (e.g., various sciurids, *Castor*).

In the other direction, the dorsal portion of the alisphenoid may be reduced to varying degrees until it comes to lie ventral to the level of the root of the zygoma or to that of the glenoid cavity. This occurs in many muroids as well as in the Hystricognathi. Within the latter, as Landry (1957, Table 2) has noted, the bathyergids do not display quite the same degree of reduction as do the others. *Incamys*, the only early Oligocene hystricognath in which this portion of the skull is known, has a low alisphenoid that extends no higher than the root of the zygoma (Figs. 12, 15A). In the Eocene *Protoptychus* the critical area is obscured, but from what is visible it would seem probable that squamosal-frontal contact had become established (Wahlert, 1973: Fig. 2). There is at present no real evidence as to whether alisphenoid reduction took place independently in the surviving hystricognath infraorders or whether the reduction represents inheritance from a common franimorph ancestor. In any event, on the basis of our present knowledge, this character can be considered no more a support for derivation of the Caviomorpha from the Thryonomyoidea than for independent derivation of the two from the Franimorpha.

(10) *Same type of squamosal-mastoid-parietal-occipital junction.* We believe that this statement refers to the presence of a lateral strip of the supraoccipital that extends downward, separating the squamosal from the mastoid process (Lavocat, 1971a: 520). It is present, but does not project freely, in all living Old World hystricognaths, being very large in bathyergids; a small blunt terminal enlargement in an old individual of *Thryonomys* is the closest approach we have seen in thryonomyoids to the projection that occurs in some caviomorphs.

In living caviomorphs, the strip is lacking entirely in the Hydrochoeridae, Dasyproctidae, Dinomyidae and Cuniculidae, and is variable in the Caviidae, being absent in *Cavia*, *Galea* and *Dolichotis*, present in *Microcavia*, and intermediate in *Kerodon*. In most echimyids it projects as a small blunt nubbin, as a blunt projection in capromyines, and culminates in the very long, independent processes of *Myocastor* and *Elasmodontomys*. Among the remaining caviomorphs, it is limited to an enclosed strip of bone. Landry pointed out that the lateral process also occurs in various sciurognathous rodent groups, "and seems . . . to be a more or less random feature among rodents" (1957: 8). It was not present in *Reithroparamys* or *Protoptychus*. *Platypittamys* appears to lack it, and it is small in *Incamys* (Fig. 12). The area is preserved in no other Oligocene hystricognaths.

It seems highly probable to us that this feature evolved independently in the Old and New World hystricognaths; certainly there is no present evidence that it did not.

(11) *Frequently, elongate cleft between auditory bulla and squamosal.* This character is highly variable. The vacuity seems usually to develop from the vicinity of what Wahlert (1974b: 374) called the post-alar fissure, a foramen or foramina on or near the squamoso-tympanic junction anteriorly; he believed that it transmits a vein tributary to the jugular sinus system. All stages from absence, through a small foramen, to a complete cleft can be seen among living Old World hystricognaths, and the caviomorphs as a whole are just as varied. The cleft does not occur in *Incamys*, *Reithroparamys* or *Protoptychus*. Among other rodents, it seems to be frequent among the Muroidea. We suspect that the varying degrees of development are related to differing stresses in the skull bones, and that this feature has no significance at higher taxonomic levels.

(12) *Maxillary reaches the rear of the floor of the orbito-temporal fossa.* We find this a rather vague characterization, and are not sure what Lavocat was trying to say. We believe that he was referring to this feature earlier on the same page (1973: 168) when he stated that "Nous avons récemment montré (Lavocat, 1972) que les relations du maxillaire et du palatin dans la région du plancher de la cavité orbitaire sont comparables." Unfortunately, he does not include the 1972 paper in his list of references, and we have been unable to locate it. We suspect that this was a reference to Lavocat, 1971b, which he likewise does not cite, but which does discuss this area of *Paramys delicatus*. It is difficult to be sure just what he meant, especially when he stated (Lavocat, 1971b: 119) that Wood (1962a) "ne montre en effet aucune suture séparant le palatin du maxillaire au niveau du trou sphénopalatin." It would seem quite clear to us that Wood (1962a: Fig. 3A) does show a suture separating the palatine from the maxillary in this area, and he specifically stated (1962a: 14) that "The maxillo-palatine and maxillo-orbitosphenoid sutures run behind the rather large sphenopalatine foramen . . . ." Later on the same page, he stated "Within the orbit, all specimens, except the type of *P. copei*, are broken so that the suture between the palatine and the orbitosphenoid cannot be located. In [that] form, however, it can be seen to run from the posterior tip of the maxillary posterodorsally into the foramen lacerum anterius." In *Ischyrotomus*, the palatine is fused with the orbitosphenoid, and is clearly separated from the maxillary (which includes the sphenopalatine foramen) by a suture (Wood, 1962a: 189, Fig. 71C). The description that Lavocat gives (1971b: 118) for the situation in *Thryonomys* seems to be almost exactly the same as that in the paramyids.

It would seem, therefore, that what Lavocat was trying to say was that the hystricognaths have retained the primitive rodent condition. This does not seem to be valid evidence of a thryonomyoid ancestry for the caviomorphs.

(13) *Habitual presence of an interparietal.* This bone is no doubt present embryologically in all members of the order. Thereafter it may remain distinct, fuse with the parietals, the supraoccipital or both, again, we suspect, in relation to skull stresses. All stages of fusion, or lack of it, are met with in both caviomorphs and Old World hystricognaths, as well as in all other rodents. A separate bone is present in the adult, among the pertinent fossils, in *Reithroparamys* (Wood, 1962a: Fig. 41A), *Protoptychus* (Wahlert, 1973: Fig. 2), *Paraphiomys* and *Diamantomys* (Lavocat, 1973: Figs. 3C, 4B). There is no trace of a separate element in *Incamys* (Figs. 7, 8) or in any of the Santacruzian genera figured by Scott (1905), but it was clearly distinct in *Platypittamys* (Wood, 1949: Fig. 1). "Habitual presence of an interparietal" is more descriptive of the Muroidea than of hystricognaths. The character has no significance at higher

taxonomic levels. Lavocat (1971a: 520) and Hoffstetter (1975: 512) apparently agreed with us on this point.

(14) *Lacrimal foramen within the orbit and not on the muzzle in front of the zygomatic arch.* Lavocat was correct in his observation: the Old World hystricognaths and caviomorphs share this character, but they also share it with most other rodents, including the Paramyidae, all other protrogomorphs, all the Franimorpha, *Castor, Pedetes,* anomalurids, sciuroids, etc. A forward displacement of the foramen occurs in muroids, glirids and dipodids. The intraorbital position was certainly a primitive rodent character retained by, among many others, the Bathyergoidea, Thryonomyoidea, Hystricidae and Caviomorpha.

(15) *Skeleton: same type of tibia in* Platypittamys *and* Paraphiomys. Lavocat described the tibia of *Paraphiomys* (1973: 91–92), but made no comparisons whatsoever with that of *Platypittamys.* We could find no indication in his 1973 paper as to what he meant, but, earlier (Lavocat, 1971a: 521) he had stated that the arching ("cambrure") of the tibia in *Platypittamys* was similar to that in Old World forms. This does not seem to us to be very significant, in which conclusion Hoffstetter (1975: 513) appears to agree with us.

(16) *Same type of brain.* Lavocat (1973) gave no documentation for this statement, and again we are not sure what he intended to imply. Earlier (1971a: 521) he stated that, while most rodents have smooth brains, a large number of caviomorphs have suggestions of fissuration, which are also present in *Thryonomys* and *Paraphiomys.* In his monograph on the East African Miocene rodents, Lavocat described (1973: 36–37) endocasts of *Paraphiomys pigotti, P. stromeri* and *Diamantomys luederitzi,* only the first of these being illustrated (1973: Pl. 1, Fig. 3; Pl. 35, Figs. 1, 3, 5, 6), and he made comparisons, among living forms, only with *Thryonomys,* for which he figured a plastic endocast (1973: Pl. 35, Fig. 2). No comparisons were made with the brains or endocasts of any caviomorphs, and there was no discussion of any of the literature. Unfortunately, we found that most of the details that Lavocat described in the text were not recognizable on his plates.

Hoffstetter (1975: 522) thought that there was a particularly marked tendency toward gyrencephaly in the hystricognaths, and that perhaps there was "una tendencia precoz, posiblemente heredada del antecesor común de los Phiomorpha y Caviomorpha." This last statement is very close to our opinion, although perhaps we differ from Hoffstetter as to what was the common ancestor.

A series of papers by Pilleri (1959a–1959j; 1960a–1960f; 1961a, 1961b; 1962) indicate that, in general, brains of sciuromorphous rodents are more advanced in gyrencephaly than those of myomorphous ones and less advanced than those of hystricognaths. The distinctions among them seem to be largely ones of degree. These degrees of complexity are, again in general, in agreement with the individual size attained by members of these groups, sciuromorphous rodents being on the average larger than myomorphous ones and smaller than hystricognaths. The Muroidea, currently the most successful and widely distributed of the major rodent groups, have brains, so far as known, with smooth neopallia. Study of rodent brains began with those of murids and sciurids, and the impression that rodent brains were all of simple type became established early. *Hydrochoerus* was noted as an exception to the general rule by Dareste (1855). Subsequently, Beddard (1892) described or mentioned the brains of a number of larger rodents in which there were cerebral convolutions.

Landry (1957: 20–22) considered that, among rodents, cerebral convolutions are positively associated with increased size, but are probably more often present in hystricognathous forms than in sciurognaths of corresponding size. Pilleri (1959b: 77) pointed out that with decrease in relative brain size (approximately the equivalent of increase in body size) the gyrencephaly progressively increases, but that the cane rat *Choeromys* (=*Thryonomys*) *harrisoni* is an exception, being less convoluted than would be expected on the basis of its relative brain size.

Pilleri's illustrations show convolutions to be present in: *Marmota* (1959a: Fig. 8), *Castor* (1959a: Fig. 10; 1959e; 1959i; 1959j), to a slight degree in *Aplodontia* (1960a: Fig. 16), *Sciurus niger* (1960b: Fig. 1), slightly in *Citellus* (1960b: Fig. 5), and in all hystricognaths that he studied (except *Heterocephalus* and *Petromus*), namely *Hystrix, Atherurus, Cavia, Dolichotis, Lagostomus, Chinchilla, Myocastor* and *Choeromys* (=*Thryonomys*) (1959b, 1959d), *Myoprocta, Dasyprocta* (1959f, 1959g, 1959h), and *Paradolichotis*, although that form, included by some in *Dolichotis*, is less convoluted than *Dolichotis* (1959g). The only possible exception that he found was *Erethizon* (1959b: 53), although the brains of this form that he illustrated the following year (1960e: Fig. 1) look convoluted. He stated, however, that the brain was smooth (1960e: 370). The brain of *Heterocephalus*, in contrast to those of most genera just discussed, is smooth; resemblances to the brain of *Geomys* were pointed out by Hill *et al.* (1957: 503) and to that of *Aplodontia* by Pilleri (1960a: 30–31). The *Heterocephalus* brain (the only bathyergid described by Pilleri) seems quite different from those of all other hystricognaths so far studied, and impressed Pilleri (1960f) as being very primitive. Later, Pilleri (1962: 494) indicated that the brain of *Petromus* was much more primitive than the brains of the caviomorphs that he had studied, and that *Petromus* and *Thryonomys* "haben sich frühzeitig von den *Ischyromyiden* getrennt und sind heute unter Bewahrung dieser primitiven hirnmorphologischen Merkmalen nur auf den afrikanischen Kontinent beschränkt."

Pilleri (1962: 494) also stated that there was a striking resemblance between the asulcate brain of *Petromus typicus* and that of the ctenodactylid *Pectinator specki* (1962: 494), that "*Pectinator* und *Petromus* stammesgeschichtlich gemeinsame Wurzeln haben" (1962: 495), and that "the brain of *Pedetes caffer* . . . shows unmistakable relationships to the Hystricomorpha" (1960d: 382). Since both *Pectinator* and *Pedetes* are sciurognaths, either brain structure is not always a good guide to rodent relationships, or the structure of the angular process of the mandible is not. Dräseke (1929: Fig. 3), however, illustrated a brain of *Pedetes* with an incomplete sulcus lateralis on each hemisphere. It looks as much like that of *Castor* as like most of the hystricognath brains figured by Pilleri.

An interesting point is suggested by the data so far available. No clear evidence of neopallial fissuration is met with in rodents with a head and body length (hbl) of less than about 350 mm, at which size a rudiment of the parasagittal (or longitudinal) fissure may appear. Very few sciuromorphous and even fewer myomorphous rodents attain a hbl of 350 mm or more. The largest sciurid whose brain is known, *Marmota flaviventris* (hbl 470–700), has a depression (Grübchen) running lengthwise that is the homolog of the sulcus lateralis (Pilleri, 1960b: 60). In *Castor* (hbl 735–1300), there is a sulcus lateralis that may be either a simple groove 15–22 mm long (about 30–45% the length of the cerebrum), or it may be subdivided into two or three parts by short breaks in its course (Pilleri, 1959c: 103, 1959e: Fig. 2). Likewise, the largest myomorphous rodent whose brain is known, *Hypogeomys* (hbl to 350), has a short sulcus lateralis and is, as a whole, "rather highly differentiated for a member of the . . . Myomorpha" (Pilleri, 1961a: 430).

Greater fissural complication frequently accompanies increase in size. The only possible exception known to us may be *Octodon* (hbl 125–195). Beddard (1892: 609) stated that the brain of this animal possesses a parasagittal (longitudinal) fissure, but gave neither a figure nor further description. Since other parts of his work do not agree entirely with reports of later investigators—Dräseke (1942) for *Capromys* and *Coendou* and Pilleri (1959b: 60; 1959f; 1959g; 1959h) for *Dasyprocta* and *Cuniculus*, who found certain neopallia to be simpler than indicated by Beddard—we believe that Beddard's report on *Octodon* requires confirmation.

Endocasts, so far as we are aware, have never been described for fossil caviomorphs, so fossil and Recent Old World hystricognath brains can only be compared with those of Recent New World genera. The endocast of *Paraphiomys* (Lavocat, 1973: 36–37; Pl. 1, Fig. 3; Pl. 35, Figs. 1, 3, 5, 6) does not look much like that which he figured for *Thryonomys* (Lavocat, 1973: Pl. 35, Fig. 2), but is closely similar to the actual brains of *Choeromys* (=*Thryonomys*) *harrisoni* (Pilleri, 1959b: Fig. 12) and of *Anomalurus pusillus* (Pilleri, 1959a: Fig. 14). The endocast of *Paraphiomys* is also similar to that of *Pseudocylindrodon texanus* (Wood, 1974a: Fig. 16), an Oligocene franimorph.

In general, we conclude that: (1) the brains of large rodents tend to be more convoluted that those of small ones; (2) the brains of hystricognaths are apt to be somewhat more convoluted than those of sciurognaths of the same size; and (3) at the present time our knowledge of brain form in rodents and its taxonomic value leaves much to be desired. As a caveat, we note that Pilleri (1960e: 375) reported that study of six brains of *Erethizon dorsatum dorsatum* from two localities in Michigan showed great variability in the form of the cerebral hemispheres. He also considered that the similarity of the brains of *Heterocephalus* and *Aplodontia*, together with the presence in each genus of two superior venae cavae, suggests a phylogenetic relationship (Pilleri, 1960a: 34—summary), a suggestion that will not appeal to many students of the order.

(17) *Same type of upper and lower molars in the Deseadan* Eosteiromys *and the Phiomyidae. Same type of primitive premolar in certain Fayum phiomyids and certain Deseadan caviomorphs.* We assume that Lavocat's use of the Colhuehuapian *Eosteiromys* was a *lapsus calami* for the Deseadan *Protosteiromys*. The following discussion, however, applies whichever genus he meant. For the terminology that we use for the parts of the cheek teeth, see Figs. 1–2, pp. 376–377).

General. The most detailed argument for close dental similarity between the Caviomorpha and Old World hystricognaths was made by Stehlin and Schaub (1951), who based their entire philosophy of rodent interrelationships, as spelled out later by Schaub (1953a, 1953b, 1958) on the supposedly fundamental importance of a tooth pattern consisting of five transverse crests in the upper molars (the "*Theridomys-Trechomysplan*"), the fifth crest (the mesoloph, the last of the five to evolve) occurring in the center of the tooth, as in the upper teeth of *Phiomys* and *Metaphiomys* (Fig. 30C,D,F). This pattern is exceedingly common among rodents and is a dental adaptation that occurred independently many times throughout the order (e.g., Theridomyoidea, Eomyidae, Cricetidae if not derived from eomyids, Dipodoidea, Castorimorpha, Anomaluridae, and whatever number of hystricognaths developed it independently). This pattern, we believe, is an adaptation to the need for an increased chewing area in animals that had reduced the cheek teeth at least to P_1^{2-1}, M_3^3 before a shift to the consumption of harsh food led to strong selective pressures for more efficient grinding surfaces. If this is correct, it should come as no surprise to anyone familiar with rodent evolution that a superficially similar and functionally identical tooth pattern should have evolved in both the

Caviomorpha and Old World hystricognaths as a reaction to the same selective pressures. This, in itself, cannot be taken as evidence of relationship below the ordinal level.

We have argued in detail (1959: 407–412) against the postulate that the "*Theridomys-Trechomysplan*" had the basic importance that Schaub believed, and we see no need to repeat all our arguments, since we feel that no evidence has been brought to bear against them. Lavocat's argument for a dental identity of early caviomorphs and thryonomyoids arises, we believe, from an acceptance of a common ancestral five-crested pattern as the basis for much of rodent dental evolution. Such a point of view (due in our opinion to a mistaken belief that the pentalophodont Theridomyoidea, so important in the European Eocene and Oligocene, could not have died out without issue) has often been implicit in work on rodent evolution by European students since the days of Schlosser, who considered (1884b: 102–105) that the theridomyoids were not only ancestral to the Hystricidae and Caviomorpha, but also (likewise on the basis of equal similarities of the tooth structure) to the Castoridae. Lavocat, not citing Schlosser's earlier work, stated (1976: 84) that "Frappé de son côté des resemblances dentaires également très étroits, Schlosser (1911) avait proposé l'hypothèse d'une origine Theridomyidae du genre *Phiomys* de l'Oligocène du Fayoum" (as indicated by Wood, 1968: 34, the specimens figured by Schlosser, that he referred to *Phiomys*, were actually *Metaphiomys schaubi* and *Gaudeamus aegyptius*).

Schaub's Pentalophodonta (1953a) has much in common with a phylogenetic tree offered more than half a century earlier by Schlosser (1884a: 327); the "*Theridomys-Trechomysplan*" of Stehlin and Schaub (1951) could be said to be merely an expansion and up-date of this diagram. As recently as 1971, Lavocat (1971a: 518) believed that there were too many differences between the thryonomyoids and the theridomyoids (such as that the latter were sciurognathous) for anyone to admit a close relationship between the two. However, later (Lavocat, 1976: 84–86) he has returned at least part way toward the Schlosserian view point in his advocacy—mistaken in our opinion—of a relationship at some stage between the Thryonomyoidea and the sciurognathous Theridomyoidea. Lavocat, however, apparently does not follow Schlosser (1884b: 102–105) in deriving the Castoridae from the Theridomyoidea.

In contrast to Schlosser and Lavocat, Stromer, the first student of significant quantities of Miocene African rodents, questioned relationships between thryonomyoids and caviomorphs. "Die mir vorliegenden Reste lassen sich, soweit vorläufig bestimmbar, fast alle mit *Hystricomorpha* im weitesten Sinne am besten vergleichen, scheinen jedoch bemerkenswerter Weise keiner südamerikanischen rezenten oder fossilen Form besonders nahe zu stehen, sondern vielmehr Formen aus dem Oligozän Ägyptens und Europas, die leider wie sie fast sämtlich ungenügend bekannt sind" (1926: 147–148).

For our part, we feel that there is not the slightest possibility of any special relationship between the thryonomyoids and theridomyoids. In this conclusion, we are merely reinforcing those formerly reached by Lavocat (1955). If such a relationship were to be established, we believe that it would demonstrate that the Suborder Hystricognathi was a wastebasket, because the Pseudosciuridae, the most primitive theridomyoids, had themselves only just originated in the middle Eocene, at a time when there were already definite hystricognaths in North America, and nothing is clearer than that theridomyoids never reached the New World and that Europe was isolated from the rest of the world during the period from quite early in the Eocene until early or middle Oligocene (Wood, 1977b: 100).

Although we think it is improbable that the theridomyoids were ever able to establish themselves outside Europe, we are not ready to abandon completely the possibility of a theridomyoid-anomalurid relationship. At least, the dental similarity between these two groups seems to us to be much greater than that between the theridomyoids and thryonomyoids or between the Thryonomyoidea and the Caviomorpha. In addition, both groups are hystricomorphous sciurognaths. Lavocat (1967: 498) has pointed out differences in middle ear structure between theridomyids and anomalurids, but the comparison was perforce between Quercy Phosphorites forms on the one hand and Recent ones on the other. Before coming to any final conclusion as to theridomyoid-anomalurid relationships, we would like some evidence from intermediate stages.

Upper Molars. We currently recognize thirteen identifiable named genera of Deseadan rodents (Table 8; *Luribayomys* and *Palmiramys* we regard as *nomina vana*), five of which (*Asteromys*, *Chubutomys*, *Litodontomys*, *Migraveramus* and *Xylechimys*) are known only from lower jaws. Of the other genera, the upper molars are four-crested in *Platypittamys* (Wood, 1949: Fig. 3A; 1974b: Fig. 2A), *Deseadomys* (Wood and Patterson, 1959: Fig. 4), *Incamys* (Fig. 17A,B) and *Sallamys* (Fig. 5A). All the known teeth of *Scotamys* are heavily worn, but it seems to us that the tooth pattern was likewise a four-crested one (Wood and Patterson, 1959: 315). In *Branisamys*, *Cephalomys*, *Protosteiromys* and the undescribed dasyproctid (p. 430) there is evidence of a fifth crest in the upper molars. This crest, however, was not a mesoloph, but originated from the anterior slope of the posteroloph, being what we call the neoloph. *Protosteiromys* (Wood and Patterson, 1959: Fig. 30) and *Branisamys* (Fig. 24B), in particular, seem to us to demonstrate this quite plainly. In five-crested Deseadan caviomorphs, the third crest from the front, the metaloph, even when interrupted in its course, is as high and as extended buccally as the protoloph, whereas, in five-crested Fayum genera (Fig. 30C,D,F), the third crest, which is certainly the mesoloph, is lower and less extended buccally than the protoloph. The fourth crest from the front in Fayum forms, the metaloph, is as high and as buccally situated as is the protoloph, just as is the third crest, the metaloph, in the caviomorphs.

Among known early Miocene thryonomyoids there is considerable variation in mesoloph development, the crest ranging from low and little extended buccally (*Myophiomys*, Lavocat, 1973: Pl. 42, Fig. 5; *Paraphiomys*, *op. cit.*: Pl. 26, Figs. 2–5; Pl. 44, Fig. 7) through low and moderately extended (*Andrewsimys*, *op. cit.*: Pl. 42, Fig. 4), low and well extended (*Phiomys*, *op. cit.*: Pl. 41, Fig. 6) to high and well extended (*Kenyamys*, *op. cit.*: Pl. 27, Fig. 5; *Simonimys*, *op. cit.*: Pl. 42, Fig. 3; *Epiphiomys*, *op. cit.*: Pl. 42, Figs. 1–2; and *Diamantomys*, *op. cit.*: Pl. 25, Fig. 7). This variability is what one would expect given the structural ancestry represented by the Fayum thryonomyoids. The mesoloph of five-crested thryonomyoids is an evolving, not degenerating, crest; it is a specialized character, not a primitive one.

Lavocat's charge (1973: 169) that our hypothesis that the four-crested upper molars of *Platypittamys* and other four-crested Deseadan genera were primitive skirts the possibility that the four-crested conditions could have been derived by simplification from a five-crested one is, of course, correct, but it would seem to us highly surprising if most genera that possessed brachyodont, primitive-looking cheek teeth had indulged in such a simplification. We believe that there is considerable evidence in support of our position. Even if there were no such evidence, Occam's Razor would argue against acceptance of Lavocat's contention without some supporting documen-

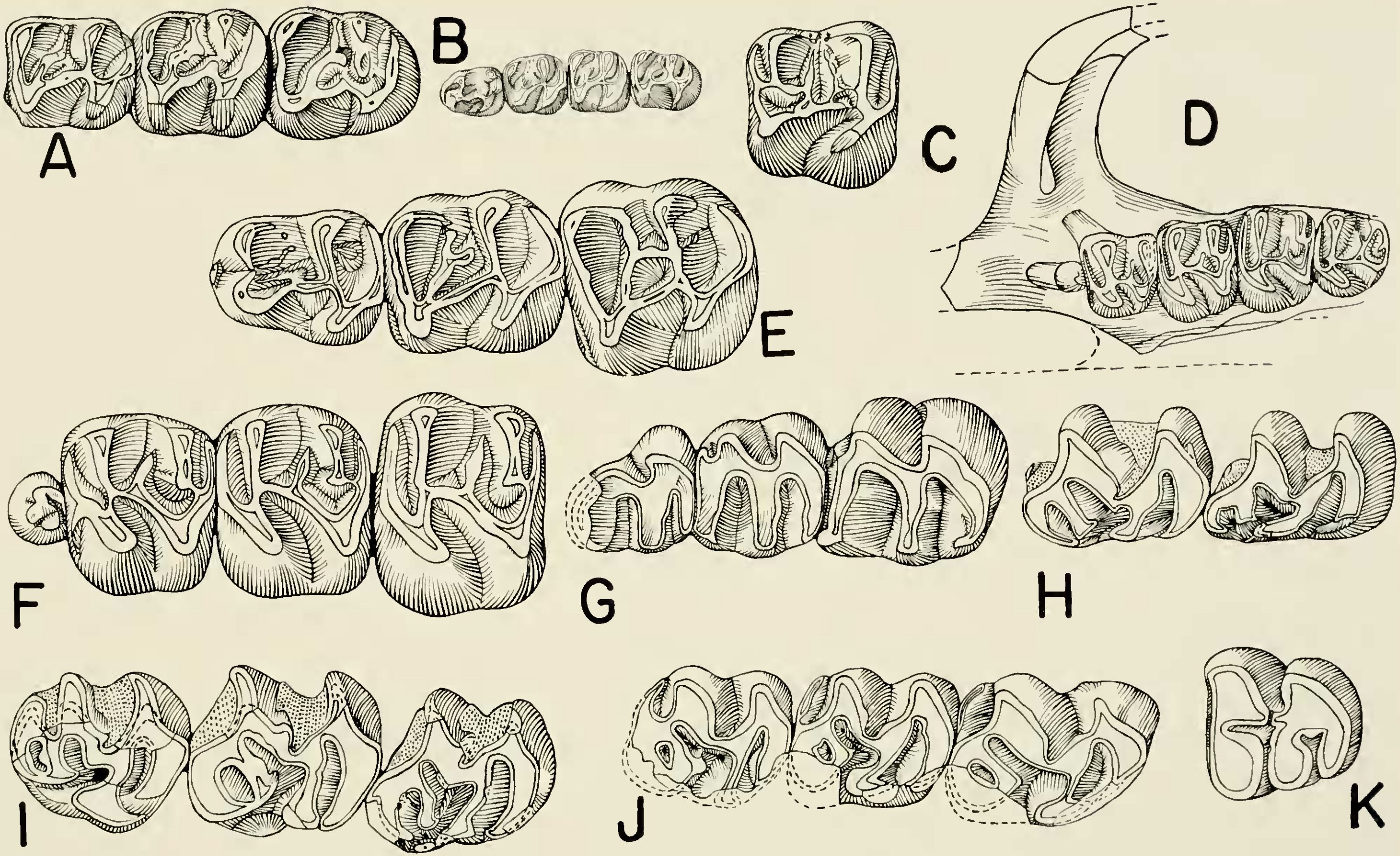

Figure 30. Cheek teeth of some Oligocene and Miocene thryonomyoids. A, C, E and F, ×10; others, ×5. A. *Phiomys andrewsi*, LM_{1-3}, YPM no. 18021; Wood, 1968, Fig. 2A. B. *P. andrewsi*, LP_4–M_3, YPM no. 18071; Wood, 1968, Fig. 1D. C. *P. andrewsi*, RM^2, YPM no. 18035, anterior end to the right; Wood, 1968, Fig. 2D. D. *Metaphiomys schaubi*, dm^{3-4}, M^{1-3}, YPM no. 21309; Wood, 1968, Fig. 6A. E. *M. schaubi*, Ldm_4–M_2, YPM no. 21310; Wood, 1968, Fig. 10E (erroneously labelled "right" in that paper). F. *M. schaubi*, Ldm^{3-4}, M^{1-2}, YPM no. 21320; Wood, 1968, Fig. 11B. G. *Neosciuromys africanus* Stromer, type, Rdm_4–M_2, Munich no. 1926x13 (=*Paraphiomys pigotti*, fide Lavocat, 1973:22). H. *Pomonomys dubius* Stromer, RM_{1-2}, Munich no. 1926x506. Dotted areas are cement. I. *P. dubius* Stromer, type, Rdm_4–M_2, Munich no. 1926x23. Dotted areas are cement. J. *Diamantomys luederitzi* Stromer, type, RM_{1-3}, Munich no. 1926x22. K. *Bathyergoides neotertiarius* Stromer, type, RM_2, Munich no. 1926x17.

tation, which we believe is entirely absent. We believe that the only basis for assuming that the caviomorph tooth pattern was derived from that of the thryonomyoids is the prior assumption that thryonomyoids were the ancestors of the caviomorphs.

If, as we believe, the Caviomorpha were descendants of franimorph reithroparamyids, their upper cheek teeth must ultimately have been derived from a four-crested ancestral stage of the type seen in *Protoptychus* (Wilson, 1937: Fig. 1) or cylindrodonts (Wood, 1973: Fig. 3), and we consider it supererogatory to assume an intermediate five-crested stage between ancestral and descendant four-crested ones until there is real evidence that such a stage actually existed.

Upper Premolars. Lavocat (1973) has greatly confused the discussion of premolar resemblances by referring to the teeth, in front of the permanent molars, indiscriminately as D (=deciduous molar) and P (=permanent premolar). In particular, he discussed the deciduous teeth of *Metaphiomys* and the probable permanent premolar of *Gaudeamus* together (1973: 170), with no indication that they were probably not homologous teeth. As a result, we do not know whether his statement that there was the "même type de prémolaire primitive dans certains Phiomyidae du Fayoum et certaines formes du Deseado" (1973: 168) was based on the comparison of permanent premolars, deciduous molars, or the deciduous molars of the African forms with the permanent premolars of the Caviomorpha. Unfortunately, although one would not get this impression from Lavocat (1973), the single tooth of *Gaudeamus* (if it is P^4 and not dm^4) is all that there is to go on as to what the upper premolars of the thryonomyoids were like, and that one tooth comes from one of the most specialized of the Fayum genera. In a later paper (Lavocat, 1978), he says very little about the antemolar cheek teeth of thryonomyoids, although he does state that P^3 or dP^3 are present in some forms (1978: 71, 78), and he included in his definition of the Family Phiomyidae (*op. cit.*: 71) the statement "Milk teeth with delayed replacement in some forms, persistent in others . . . ." He does not mention that replacement of deciduous teeth is unknown in all other thryonomyoids.

Upper premolars are known in seven of the Deseadan genera. The tooth is incipiently five-crested in *Branisamys* (Fig. 23C,F); four-crested in *Incamys* (Figs. 17A, 18C) and *Sallamys* (Fig. 4A); three-crested in *Deseadomys* (Wood and Patterson, 1959: Fig. 4A), *Cephalomys* (Wood and Patterson, 1959: Figs. 13A, 14A,B) and *Platypittamys* (Wood, 1949: Fig. 3A,B); and probably three-crested in *Scotamys*. The teeth of the three-crested forms look primitive to us, and we believe that these teeth are close to the ancestral caviomorph condition.

Upper premolars of thryonomyoids are unknown except for the one specimen of *Gaudeamus aegyptius* that is more probably P^4 than dm^4 (Wood, 1968: Fig. 14A and Table 2). All other antemolar upper cheek teeth (except for the peg-like dm^3 or P^3) known among thryonomyoids from the early Oligocene to the present are dm^4. The premolar of *Gaudeamus* is a three-crested tooth and, as Lavocat has stated (1973: 170), it shows some similarity to that of *Platypittamys* (Wood, 1949: Fig. 3A,B), although the two are far from identical and, if one were to have been derived from the other, that of *Platypittamys* seems obviously to be the more primitive in that it is much more brachyodont, the cusps are more distinct, and the crests are less fully developed. The permanent premolars of both *Platypittamys* (Wood, 1949: Fig. 3A,B; 1973b: Fig. 2A,B) and *Gaudeamus* (Wood, 1968: Fig. 14A) could have been derived from one like that of the hystricomorphous franimorph *Protoptychus* (Wilson, 1937: Fig. 1).

Lower Molars. The lower molars of *Phiomys*, the most primitive known thryonomyoid, were shown by Wood (1968: 32–33) to vary widely as to crest number. Within this primitive genus can be found "a complete sequence from five-crested specimens of *Ph. andrewsi* through four-crested ones of the same species, to the nearly three-crested ones of *Ph. paraphiomyoides* and of *Ph. lavocati*. Since the first and last of these species are contemporaneous animals, it is possible to assume either that evolution is proceeding from five-crested to three-crested, or the reverse sequence, or from four-crested in both directions." Wood's preference was for the last of these choices: "the four-crested would be the most primitive, and evolution would be in both directions, toward simplification or complication." We adhere to this interpretation. If Wood was correct on this point, this alone would rule out any possible relationship between the thryonomyoids and the theridomyoids. It would also support the idea of parallel evolution of the Thryonomyoidea and Caviomorpha from northern hemisphere franimorphs that had four-crested molars. Among the early Miocene thryonomyoids, the number of crests is either four or three. A point that must be stressed here is that in those early thryonomyoids that were "experimenting" with five-crested lower molars, the fifth crest (the third from the front) is certainly a mesolophid; in some individuals traces of a mesoconid and (rarely) of a metastylid can be seen.

The lower molars of Deseadan rodents are generally four-crested (*Asteromys*, *Branisamys*, *Cephalomys*, *Chubutomys*, *Incamys*, *Migraveramus*, *Platypittamys* and *Protosteiromys*). In *Xylechimys* (Patterson and Pascual, 1968: Fig. 2A) and *Deseadomys arambourgi* (Wood and Patterson, 1959: Fig. 5) the teeth are intermediate between being four-crested and three-crested, and *D. loomisi* is three-crested, one of the crests, the metalophid, of the four-crested forms having been lost (Wood and Patterson, 1959: 311, Fig. 7). The teeth of *Sallamys* (Fig. 5D–F) seem intermediate in this respect between those of the two species of *Deseadomys*. The lower molars of the known specimens of *Litodontomys* and *Scotamys* are too worn to permit certain determination of the number of crests, although the teeth are compatible with there having been four. There is, therefore, no evidence that early caviomorph lower molars were ever five-crested; no known lower molar of any Deseadan rodent shows any indication of a mesoconid, a mesostylid or a mesolophid. When, as in some specimens of post-Deseadan erethizontids, an incipient fifth crest develops on the lower molars, it arises from the posterior face of the anterolophid (Wood and Patterson, 1959: 381), not from the ectolophid, and hence is completely unrelated to the fifth crest of thryonomyoids.

A striking feature of the lower molars of nearly all thryonomyoids is the presence of an anteroexternal basal cingulum. Among the Fayum forms it is present in *Phiomys* (Fig. 30A,B; Wood, 1968: Figs. 1; 2A,B; 3A,B; 4A) although very small or absent in *P. lavocati* (Wood, 1968: 47; Fig. 5A,C,D), small in *Paraphiomys simonsi* (Wood, 1968: Fig. 5F), transferred below (p. 520) to *Neosciuromys*, but large in *Metaphiomys* (Fig. 29E; Wood, 1968: Figs. 8–10, 12H, 13A) and *Phiocricetomys* (Wood, 1968: Fig. 16A,D). This last genus is peculiar among thryonomyoids in having but three lower cheek teeth, either dm_4–M_2 or M_{1-3} (see p. 521). The second tooth has a very heavy anterior cingulum that extends back along the buccal face of the tooth and the buccal half of the posterior face; cuspules occur here and there along its length. In the last tooth, the cingulum, very heavy and with cuspules, reaches posteriorly to the hypoconid, and in the first is limited to the base of that cusp. Only in *Gaudeamus*, a specialized form, is the anterior cingulum entirely lacking (Wood, 1968: Figs. 14E,G,H; 15B–E,G).

An anterior cingulum, like that of *Phiomys* and *Metaphiomys*, is very prominent among the Miocene thryonomyoids (Fig. 30G–J; Stromer, 1926: Pl. 41, Figs. 24, 25C, 32C; Pl. 42, Fig. 28; Lavocat, 1973: Pl. 25, Fig. 6; Pl. 26, Figs. 7–10; Pl. 27, Figs. 1, 3, 4, 9; Pl. 28, Figs. 1, 2, 4, 11–13). These cingula are prominent and elevated in *Petromus* (Wood, 1962b: Fig. 1E,F), but are absent in *Thryonomys* (Wood, 1962b: Fig. 2A–C) as in its probable ancestor *Gaudeamus*.

There is no trace of such a basal anterior cingulum in any bathyergoid (Lavocat, 1973: Pl. 29, Figs. 5–6; Pl. 30, Figs. 1–6), hystricid or caviomorph, so far as we are aware. This feature, by itself, it seems to us, rules out all known thryonomyoids (except *Gaudeamus*, which, of course, is much too advanced in the cresting of its cheek teeth to be a possible caviomorph ancestor) from possible ancestry to any caviomorph, hystricid or bathyergid. The presence of this cingulum on the molars of thryonomyoids means that any thryonomyoid that could, morphologically, have been ancestral to the caviomorphs must be a hypothetical Eocene form with an assumed set of characters quite different from those of any known member of the superfamily. We consider it highly doubtful that such a hypothetical form could be included in the Thryonomyoidea. We believe it would have been a franimorph. The Chapattimyidae (Hussain *et al.*, 1978) do not fill the requirements for such an ancestral form, nor do their lower teeth possess an anterior cingulum of the sort found in the Thryonomyoidea.

Lower Premolars. The lower premolars of thryonomyoids are unknown except for those described by Wood (1968: Figs. 1B,D; 14E) from the Jebel el Qatrani Formation (Fig. 30B). He was able to find only 3 permanent lower premolars (P_4) as compared with 57 deciduous ones (dm_4) in the material at his disposal. The only species in which there certainly was replacement of the deciduous tooth by its permanent successor was *Phiomys andrewsi*, the most primitive known thryonomyoid, and in this form replacement was delayed long after the normal time of replacement. The single permanent lower premolar of *Gaudeamus* was uncovered, deep within the jaw, when the deciduous tooth was removed from above it (Wood, 1968: 72); whether or not it would ever have erupted is unknown; certainly eruption would not have occurred until rather late in life. All three known Fayum specimens of P_4 are from the lower fossil wood zone and all have essentially the same pattern. There is no suggestion of an anteroconid on any of them. The metaconid is the highest element of the anterior part of the tooth, and is continued anteriorly by a cingular arm that crosses in front of the protoconid in one specimen of *Phiomys andrewsi* (Wood, 1968: Fig. 1D) and in *Gaudeamus* (*op. cit.*: Fig. 14E). There may (*P. andrewsi*) or may not (*Gaudeamus*) be a mesoconid. There is a complete ectolophid in *P. andrewsi*, but none in *Gaudeamus*. The entoconid is completely isolated in all three teeth, except from the posterolophid through which it is connected with the hypoconid.

In the Deseadan Caviomorpha, P_4 primitively had a complete ectolophid (*Asteromys*, *Cephalomys*, *Deseadomys*, *Migraveramus*, *Platypittamys* and *Sallamys*), but progressively it became interrupted (*Incamys*, Fig. 19C–E). There is no anteroconid in *Asteromys* (Wood and Patterson, 1959: Fig. 26A), *Deseadomys* (*op. cit.*: Fig. 5), *Platypittamys* (Wood, 1949: Fig. 3C–D; 1974a: Fig. 2C–D) or *Sallamys* (Fig. 5C). There is no anterior arm of the metaconid nor a mesoconid in any of these genera. The entoconid may be connected directly with the hypoconid with no posterolophid (*Platypittamys*); through the hypolophid with a distinct, isolated, posterolophid (*Cephalomys* and *Sallamys*); only through the posterolophid (*Deseadomys*); through both the hypolophid and posterolophid

(*Asteromys* and *Migraveramus*); or there may be no hypoconid-entoconid connection at all until after very considerable wear (*Incamys*).

Of all the Deseadan lower premolars, the closest to those of *Phiomys* are those of *Platypittamys*. We believe that this is because the former is close to the primitive thryonomyoid pattern and the latter close to the primitive caviomorph one, and that both the thryonomyoids and caviomorphs were descended from primitive (and hence similar) franimorph ancestors that had four-crested lower premolars. Lavocat (1973: 169–170) has argued that, in general, the cheek teeth of *Platypittamys* were not primitive. We disagree with him on this. Slightly later (*op. cit.*: 170), Lavocat stated that the structure of P_4 of *Deseadomys* and *Platypittamys* is fundamentally identical to that of *Phiomys andrewsi* and, hence (as we interpret his meaning), primitive. But we do not see how it is possible for the pattern of P_4 of *Platypittamys* to be considered to be primitive without also accepting the upper and lower molars and the upper premolar of *Platypittamys* as primitive. If this be done, the patterns of P_4 might suggest close caviomorph-thryonomyoid relationships, but the patterns of the other cheek teeth would demonstrate the absence of such affinities. We know of nothing that would interfere with the derivation of P_4 of *Asteromys, Cephalomys, Deseadomys, Migraveramus, Platypittamys* or *Sallamys* from those of cylindrodonts (Wood, 1973: Fig. 5A) or, ultimately, of *Franimys* (Wood, 1962a: Fig. 49A) or *Reithroparamys* (*op. cit.*: Fig. 42B).

Thus, while we agree with Lavocat (1973: 168) that there is the "même type de [lower] prémolaire primitive dans certains Phiomyidae du Fayoum et certaines formes du Deseado," we feel that using the similarity of premolars (based on a total Oligocene to Recent thryonomyoid sample of three teeth) and disregarding the much greater difference of pattern of the molars of the same Deseadan genera is completely unjustified.

Deciduous Teeth. The best opportunity for comparing thryonomyoid and caviomorph antemolar teeth lies in the deciduous dentition, dm_4^4. Lavocat (1976) had available both upper and lower deciduous teeth of *Incamys* and *Branisamys*, although those of the latter were broken. Although deciduous teeth are almost universally present in thryonomyoid jaws (in fact, they are never known to have been replaced by the permanent premolar after the early Oligocene of the lower fossil wood zone), they occur at about the normal mammalian frequency among specimens of Deseadan caviomorphs. Neither upper nor lower deciduous teeth are known for *Asteromys, Chubutomys, Deseadomys, Litodontomys, Luribayomys, Migraveramus, Palmiramys, Platypittamys, Protosteiromys, Scotamys* and *Xylechimys*, or 11 of the 15 named Deseadan genera. Only the lower is known in *Cephalomys* and *Sallamys*; both uppers and lowers are preserved in *Branisamys* and *Incamys*. We have therefore used materials from the Colhuehuapian and Santacruzian to supplement our discussion of the Deseadan specimens.

Hoffstetter (1975: 520) cited, as a common character shared by the Caviomorpha and Phiomorpha [=Old World hystricognaths?], the frequent retention of "uno o dos premolares y/o los dientes de leche correspondientes." We are not sure which if any of these forms retain both dm^3 and P^3, since these teeth are very difficult to distinguish in rodents (Wood, 1969; 1970b: 245–246), but this is a minor point. As Hoffstetter added, this retention of antemolar teeth excludes from their ancestry those forms that had lost these teeth. But, so far as we are aware, no one has ever proposed that either the caviomorphs or any of the Old World hystricognaths were descended from, e.g., cricetids, and we believe that Hoffstetter here was merely setting up a straw man in order to knock it down.

Upper Deciduous Teeth. Among the Oligocene Thryonomyoidea, dm^4 is known from 11 specimens of *Metaphiomys schaubi* and one of *Metaphiomys* or *Phiomys* sp. indet. (Wood, 1968: Table 2). In all of these, the tooth is five-crested, with an anteroloph, protoloph, mesoloph and a posterior marginal posteroloph, to the middle of which is connected the end of the metaloph via the lingual end of the metaconule (Fig. 30D,F; Wood, 1968: Figs. 11, 13B). This pattern is essentially identical to that of the adjacent molars.

Hoffstetter stated (1975: 520) that "*Phiomys* presènta un reemplazo normal de dP^4 por P^4." So far as we know, this statement is entirely without factual basis, and he has apparently completely misunderstood the situation in *Phiomys* (Wood, 1968: diagnosis of *Phiomys*; 39–40, 83–84). No upper premolars or deciduous molars have with certainty been reported for *Phiomys*; the only possible example of such a tooth is one specimen of dm^4, identified as "*Phiomys* or *Metaphiomys* sp. indet." (Wood, 1968: 67, Fig. 13B). We suspect that dm^4 was replaced, late in life, by P^4, simply because the corresponding replacement occurred in the lower teeth. But this would be a long, long way from "un reemplazo normal."

In caviomorphs, dm^4 is usually very similar to the molars in crown features, but may be somewhat smaller and longer and have a larger anteroloph and paraflexus. Exceptionally, as in living dasyproctids, the anterior half of the tooth may elongate and neomorph crests develop within the enlarged parafossette.

Among Deseadan caviomorphs, the tooth is best known in *Incamys* (Fig. 17A,H,I), one specimen (Fig. 17H) being essentially unworn, and another (Fig. 17I) only slightly worn. Both of these teeth clearly consist of four transverse crests, the third of which is interrupted, with no indication of a fifth crest. We believe these crests to be the anteroloph, including the protocone; the paracone-protoconule-hypocone; the metacone-metaconule-hypocone; and the posteroloph. There is no suggestion of a mesoloph, which we feel is because the Caviomorpha were derived from North (or Middle) American franimorphs in which there never was a mesoloph. The dm^4 of *Branisamys*, figured by Hoffstetter and Lavocat (1970: Fig.) is both broken and badly worn, but suggests that there had been a four-crested pattern. However, one specimen (Fig. 24B) of dm^4 of this genus clearly shows increasing complexity. There is an incipient anterior crest arising from the buccal end of the anteroloph, and the beginning of a neoloph, arising by forward growth of ridges from the middle and the lingual tip of the posteroloph. The tooth of *Incamys* seems to us to be clearly the more primitive.

This tooth is known from a somewhat larger number of Santacruzian genera. In *Neoreomys* (Scott, 1905: Pl. 65, Fig. 3), the anterior part of the tooth seems to be similar to that of *Incamys*. There is a posterior prism of enamel, with a lake in its center, which we would interpret as being homologous to the two crests in *Branisamys* that we have called the beginnings of a neoloph. In *Eocardia* (Scott, 1905: Pl. 68, Fig. 27), the tooth has acquired the typical eocardiid outline, but would seem to be composed of the same features as in *Incamys*. Scott also figured a worn dm^4 of *Neoreomys australis* (1905: Pl. 65, Fig. 4), *Stichomys regularis* (1905: Pl. 65, Fig. 19) and *Schistomys erro* (1905: Pl. 68, Fig. 26); these, however, show essentially no details of the pattern. They could be (and probably were) based on the same basic pattern as in *Incamys* and *Branisamys*.

It is clear that the fifth crest that seems to be developing in the caviomorph dm^4

(our neoloph) is a forward outgrowth from the posteroloph—absent in *Incamys*, developing in *Branisamys* and fully developed in the Santacruzian genera. We see no possibility of homologizing this crest with the metaloph of the thryonomyoid dm^4, since the neoloph of the caviomorphs was clearly in the process of development, in South America, during the Oligocene.

A tooth that is probably dm^3 rather than P^3 is represented by an alveolus in the type of *Branisamys luribayensis* (Hoffstetter and Lavocat, 1970: Fig.) and in PU no. 21955 (Fig. 24B); an intra-alveolar root in *Incamys bolivianus*, PU no. 20980 (Fig. 17I); and a worn nubbin on both sides of the skull of *I. bolivianus*, PU no. 21726 (Fig. 17A). These tell us nothing other than that a minute tooth was present. One was also present in *Metaphiomys schaubi* (Fig. 29D; Wood, 1968: Fig. 11B, Table 2); no trace of such a tooth is preserved in *Gaudeamus*. The presence of this tooth is merely a primitive rodent character. At present, we do not know, for any of the genera involved, whether this tooth was dm^3 or P^3 (Wood, 1970b: 245–246), or whether it had a pattern or was merely a conical cusp.

Lower Deciduous Teeth. The lower milk molar (dm_4) is better represented among the Deseadan Caviomorpha than is the upper, but still is known only from four genera: *Branisamys*, *Cephalomys*, *Incamys* and *Sallamys*. All three available teeth of *Incamys* are highly worn; there is no way of being certain whether the pattern was like that in the other genera, or whether it was different. The Princeton collections include a specimen of *Branisamys* with a broken dm_4 (Fig. 24G), and we believe that GB no. 014, the type of Hartenberger's *Villarroelomys bolivianus* (Figs. 26A, 31H) is also dm_4 of *Branisamys*. According to our interpretations, the pattern in both of these *Branisamys* teeth was essentially like that of *Sallamys* (Figs. 5D, 31F) or of *Cephalomys* (Figs. 26B, 31G).

The pattern of dm_4 of *Sallamys pascuali* posed a number of problems that we have touched on above (p. 390). This tooth (Figs. 5D, 31F) is obviously very complex, and closely resembles that of *Cephalomys* (Wood and Patterson, 1959: Fig. 20A,B), the only previously described unbroken Deseadan dm_4. In each, the talonid is like that of the molars, the hypoconid being continuous backward into the posterolophid and forward into the hypolophid. It is in the very complex trigonid that the differences lie. There is a continuous anteroposteriorly directed ectolophid; a cusp that we believe to be the protoconid extends backward toward the entoconid. In *Cephalomys* (Fig. 31G), the metaconid lies behind the protoconid, whereas in *Sallamys* (Figs. 5D, 31F) it is farther forward. In both, the anterior end of the tooth is formed of a multicuspidate complex that we consider to have been derived from the anteroconid. A complex anteroconid area is a rather frequent evolutionary trend in dm_4 of a wide variety of unrelated rodents.

An attempt to unravel the homologies of the parts of the teeth in these two forms has led us into an investigation of the lower deciduous teeth of later caviomorphs.

In the simplest type of caviomorph dm_4 that we have seen, the trigonid consists of buccal (protoconid) and lingual (metaconid) cusps, connected posteriorly through a metalophid and anteriorly through an anterolophid (in which the anteroconid may or may not possess some individuality), surrounding a trigonid basin or anterofossettid (*Erethizon dorsatum*, Fig. 31A). Due to the greater length of the tooth, this fossettid is larger than its serial homolog in the molars. This complex is united with the talonid by the ectolophid.

Deciduous lower molars of this sort are known in such octodontids as *Sciamys*, in early erethizontids, and in various echimyids, such as *Prospaniomys* (Figs.

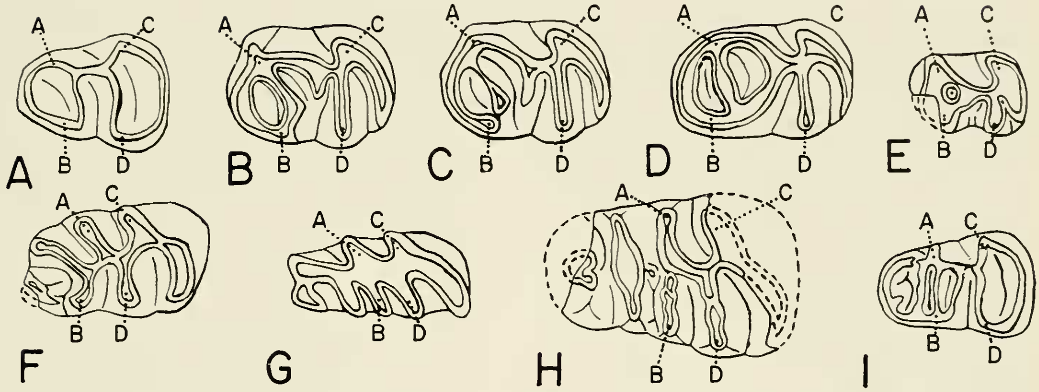

Figure 31. Sketches of lower deciduous molars (dm_4) of selected caviomorphs, not to scale; all drawn as if from the right side. A. *Erethizon dorsatum*, MCZ no. 51367. Simple pattern. B. *Protacaremys prior*, AMNH no. 29707. C. *P. prior*, FMNH no. P 13295. D. *P. prior*, AMNH no. 29692, reversed. E. *Prospaniomys priscus*, AMNH no. 29697, reversed. F. *Sallamys pascuali*, PU no. 20909. G. *Cephalomys arcidens*, ACM no. 3013. H. *Branisamys luribayensis* (type of *Villarroelomys bolivianus*), GB 014, reversed and restored. I. *Erethizon dorsatum*, MCZ no. B 7752. Complex pattern.

Abbreviations: A—protoconid; B—metaconid; C—hypoconid; D—entoconid.

5H, 31E), as variants in *Acarechimys* (for validation of this name, see Appendix 2), in *Eumysops* (Kraglievich, 1965: Fig. 2) and in the Antillean heteropsomyines (Miller, 1929: Pl. 2, Figs. 3a, 4a; Pl. 3, Fig. 1a; Pl. 4, Fig. 2a).

There have been various modifications of this pattern, ranging from relatively simple to highly complex. As examples of simple changes, we may cite: *Paradelphomys*, in which the very marked obliquity of the lophids has converted the circular anterofossettid into a slit and has greatly shortened the ectolophid without completely obscuring the primitive pattern; and *Spaniomys*, *Stichomys*, *Cercomys*, etc., in which an anteroflexid has developed between metaconid and anterolophid, thus converting the tooth into as good a replica of the molars as the upper milk tooth usually is.

Considerably greater complexity is present in *Protacaremys prior*, although AMNH nos. 29692 and 29707 and FMNH no. P 13295 are all different in details. Here there are three crests from the protoconid to or toward the metaconid (Figs. 5G, 31B–D). The anterior of these is clearly an anterolophid; the nature of the others is more uncertain. However, on the basis of variants seen in *Erethizon dorsatum*, as discussed below, we believe the posterior crest to be a metalophid resembling the mesolophid of thryonomyoids and the middle crest to be a neomorph crossing the anterofossettid. We believe that the tooth pattern of this tooth of *Prospaniomys priscus* (Fig. 31E) is basically the same.

This stage is continued, morphologically, in *Sallamys pascuali* (Figs. 5D, 31F), where the protoconid has become separated from the metalophid, and a deep buccal valley has developed as a neomorph, as has also the anteriorly facing opening, leading deep into the anteroconid. The teeth of *Cephalomys* (Figs. 26B, 31G; Wood and Patterson, 1959: Fig. 20A) and *Branisamys* (Figs. 26A, 31H) demonstrate continuations of this process, with the anteroconid now separated from the metaconid.

This description is, of course, an attempt to present a morphological series and not a phylogenetic proposal. It is obvious that there is a great deal still to be learned of deciduous tooth evolution in the early caviomorphs. We have presented our interpretation (Fig. 31) of the patterns of these teeth, suggesting one manner by which the pattern of *Sallamys*, *Cephalomys* and *Branisamys* could have been derived. We feel no great confidence in the complete accuracy of our interpretation, but, with our present lack of knowledge, it is as logical as any other.

Any interpretation of the actual evolution of dm_4 in the Caviomorpha is complicated by the extreme variability that we have observed in this tooth among Recent specimens of *Erethizon dorsatum*. Some individuals of this species (e.g., MCZ no. 51367, Fig. 31A) have the simplest caviomorph dm_4 that we have seen. There may be an anterior spur into the anterofossettid (MCZ no. 39006), a small swelling on the ectolophid (MCZ no. 39010), or a short spur in this location (MCZ no. B9975). The structures on these last two specimens look for all the world like an incipient mesoconid and an incipient mesolophid, respectively. The spur into the anterofossettid may form a continuous lophid that divides the anterofossettid into two (MCZ no. B7752, Fig. 31I), and may be joined by a secondary spur to produce three divisions of the anterofossettid (MCZ no. 8846). The apparent mesolophid may extend to the lingual margin of the tooth, where it may be connected to the posterior tip of the metaconid (Fig. 31I). There may be a second spur behind the apparent mesolophid (MCZ no. 7800). All intermediate stages in these developments are present in the MCZ collections, often within what were surely interbreeding populations. We feel complete confidence that dm_4 of MCZ no. 51367 (Fig. 31A) is a primitive tooth, and that dm_4 of MCZ no. B7752 (Fig. 31I) is a highly specialized one.

Although we do not know, we strongly suspect that this condition of extreme variability in dm_4 of *Erethizon* is a very recent development, perhaps related to the rapid spread of the genus over a broad expanse of North America in postglacial time. The more complex examples of dm_4 discussed above surely are in the process of developing a variety of neomorph crests, which, although sometimes resembling mesoconids and mesolophids, can only have developed as parallelisms to such structures in any other rodents.

The pattern of dm_4 of the Oligocene petromurids (see below, p. 523, for our usage of this term) is quite different. The rear of the tooth is the same as in the caviomorphs and other rodents, formed of the hypoconid connected anteriorly with the entoconid and posteriorly with the posterolophid. There is also a continuous anteroposterior ectolophid. But the anterior portion of the tooth is strikingly different. The anteroconid is a very minor feature of dm_4 (Wood, 1968; Figs. 1F,G; 2B; 3A,B; 4A; 5C; 8A; 9A–D; 10A,E; 12F); either the trigonid basin opens forward, or there is a deep valley between the protoconid and metaconid, which are near the front of the tooth; and there is usually a strong mesolophid (Wood, 1968: Figs. 1F,G; 2B; 8C; 9B–D; 10E; 14D,G; 15E,G), similar to the structure that apparently developed very recently in this tooth of *Erethizon*. Occasionally, the mesolophid is absent in the Fayum genera, although there is still usually a mesoconid (Fig. 30E; Wood, 1968: Figs. 3A,B; 4A; 5C,F).

Among the Miocene thryonomyoids, *Neosciuromys africanus* (Fig. 30G), *Elmerimys* and *Myophiomys* (Lavocat, 1973: Pl. 28, Figs. 11–13) have very simple dm_4, with a protoconid and metaconid connected through the anterior cingulum, but not through a metalophid. This is very similar to dm_4 of the Oligocene *Neosciuromys simonsi* (Wood, 1968: Fig. 5F), and is somewhat simpler than dm_4 of *Paraphiomys stromeri* or *P. pigotti* (Lavocat, 1973: Pl. 26, Figs. 7–10). The anterior portion of dm_4 is unknown in *Simonimys* (Lavocat, 1973: Pl. 27, Fig.

1) and does not show in the figure of *Kenyamys mariae* (Lavocat, 1973: Pl. 27, Fig. 6).

Only in *Diamantomys luederitzi* (Lavocat, 1973: Pl. 25, Fig. 6) and *Pomonomys dubius* (Fig. 30I) is dm_4 complicated. Here there are two or three cusps in the metaconid-anteroconid area, although they are very different from anything found in the Caviomorpha.

However, in the thryonomyid *Gaudeamus*, dm_4 is formed of a series of parallel transverse ridges, more like what is seen in dm_4 of *Theridomys* (Wood and Patterson, 1959: Fig. 35B) than like that in any caviomorph, where the closest approach we have seen to it is the complex Recent *Erethizon dorsatum* (Fig. 31I) or *Branisamys* (Fig. 31H). As in the Caviomorpha, the talonid is of the type usually (but not in *Gaudeamus*) found in the molars, but there has been extensive modification of the anterior portion.

Although there is similarity between dm_4 of *Gaudeamus* or of *Thryonomys* (Wood, 1962b: Fig. 2A) and those of caviomorphs, similarities as great or greater can be found elsewhere among the rodents. There is little or no difference between dm_4 of these thryonomyids and that of *Anomalurus* (Wood, 1962b: Fig. 1B); and dm_4 of the entoptychine geomyids *Gregorymys curtus* (Wood, 1936a: Fig. 13) and *Entoptychus* cf. *minor* (Rensberger, 1971: Pl. 6, Fig. i) or of *Theridomys* (Vianey-Liaud, 1972: Fig. 1) seem to us to be much closer structurally to those of the Deseadan Caviomorpha than are those of the thryonomyids. The pattern of dm_4 of thryonomyids is also reminiscent of that of *Theridomys*, but again we do not believe that it indicates thryonomyoid-theridomyoid affinities, as *Gaudeamus* is quite advanced for an Oligocene thryonomyoid, and the similarities of its dm_4 to that of *Theridomys* must be pure parallelisms, *Gaudeamus* having evolved from something like *Phiomys*. The patterns of dm_4 of the petromurids are very suggestive of those of various ctenodactylids (Wood, 1977a: Fig. 5). Needless to say, we do not consider either the entoptychines or the theridomyids closely related to the caviomorphs, nor the theridomyids and ctenodactylids to the thryonomyoids. We have merely selected examples of similar deciduous teeth in unrelated forms.

We do not see that the patterns of the deciduous teeth give any support to thryonomyoid-caviomorph relationships.

The great variability in dm_4 within the single living species *Erethizon dorsatum*, as well as that in *Phiomys* and *Metaphiomys* (Wood, 1968: Figs. 1F,G; 2B; 3A,B; 4A; 5C; 8C; 9A–D; 10A,E; 12F) shows what extremes of variability may occur when, for some reason, there is either strong selection toward increasing the complexity of a tooth, or a sudden reduction in selective pressures of any sort acting on it. We believe that this situation demonstrates our ignorance of many of the causes of evolutionary change in dm_4.

It is obvious from the above that not enough is known about lower deciduous teeth of caviomorphs to be of great significance in unravelling their interrelationships. As an aside, the evolutionary history of the deciduous teeth has been sadly neglected, not only among rodents, but in all of the Mammalia.

(18) *Multiserial Incisor Enamel* (by A.E.W.). Among rodents, there are three types of incisor enamel: the pauciserial, the primitive type, found in most Eocene rodents; and two more evolved types, uniserial and multiserial, found in later rodents (Korvenkontio, 1934). The temporal distribution of the three types makes any other relationship among the three very difficult to visualize.

"Pauciserial enamel is a good structural predecessor for uniserial and multiserial enamel. It would appear to be the ancestral condition . . . . Presumably acquisition of two layers in which the organization of prisms is different served in some way to strengthen the enamel . . . . There is no available evidence to suggest that one of the two surviving kinds is superior to the other or that one of them has ever evolved from the other" (Wahlert, 1968: 13). As indicated, there are no known cases of transition between uniserial and multiserial enamel, but, in a few cases, transitional stages between pauciserial and the advanced types have been found.

In pauciserial enamel, the inner layer consists of prisms that may or may not be organized into lamellae. The bands are of variable width, the widths lying in general between those of the uniserial and multiserial types (Wahlert, 1968: 4). "The structure appears similar to multiserial enamel but lacks the uniformity of organization. Bands are usually not inclined . . . . Some pauciserial enamels have fewer prisms per band, and thus the bands are narrower, suggesting uniserial enamel in appearance."

The bands of the inner layer of multiserial enamel are many prisms wide. They are inclined at considerably greater angles toward the wear surface of the tooth; the values given by Korvenkontio (1934: 116–123) vary from 10° to 45° in the upper incisor and from 22° to 50° in the lower.

In uniserial enamel, the bands of the inner layer are one enamel prism wide. These are inclined toward the tip of the tooth at angles that vary more than do those of multiserial enamel, ranging from 0° to 50° in both upper and lower incisors (Korvenkontio, 1934: 116–123). The uniserial type is more highly organized than either of the others, and rather strikingly different in appearance from the pauciserial, whereas "the structure [in pauciserial enamel] appears similar to multiserial enamel but lacks the uniformity of organization" (Wahlert, 1968: 4). For illustrations of the three types of enamel, see Korvenkontio, 1934: Pls. 3–27; Wahlert, 1968: Fig. 1.

The multiserial type is present, so far as has been determined, in all caviomorphs, all thryonomyoids, hystricids and bathyergids as well as in *Pedetes* and Oligocene to Recent ctenodactylids. In the anomalurids, the enamel is uniserial.

The enamel of the upper incisor of *Protoptychus* "appears to be pauciserial. Pauciserial and multiserial enamels are similar, and a transverse section is not ideal for distinguishing them" (Wahlert, 1973b: 4). In *Prolapsus*, both upper and lower incisors were pauciserial, but the bands of the lower incisors were inclined at an angle of 19° and those of the uppers at an angle of 15° (Wood, 1973: 27). That is, the enamel of *Prolapsus* was in the process of making the transition from pauciserial to multiserial.

Recently, a group of isolated teeth of ctenodactyloids has been described from the middle Eocene of Pakistan, as members of a primitive ctenodactyloid family, the Chapattimyidae (Hussain *et al.*, 1978). Isolated incisors, referred to this family, were sectioned (*op. cit.*: Pl. 7, Figs. 1–3) and studied with the scanning electron microscope. The figures clearly show a diagrammatical pauciserial pattern (cf. Hussain *et al.*, 1978: Figs. 1–3 and Wahlert, 1968: Fig. 1C), in spite of their having been identified as multiserial (Hussain *et al.*, 1978: 104). Sahni (1980: 23) also concluded that these incisors possessed pauciserial enamel.

The presence of pauciserial enamel in what are undoubtedly ctenodactyloids (very possibly ctenodactylids) from the Eocene of Pakistan is of considerable importance in demonstrating that, even if there should turn out to be a distant relationship between ctenodactyloids and hystricognaths (which is an unproven hypothesis), multiserial enamel must have originated in the ctenodactylids independently of its origin in the various hystricognath groups. The suggestion by Hussain *et al.* that their Chapattimyidae were ancestral to the Hystricognathi, including the cylindrodonts, as well as the Ctenodactylidae, is discussed below (p. 515) and rejected.

As with so many of the important morphologic features that characterize the hystricognaths, there is a shortage of fossils representing the intermediate stages between the primitive (pauciserial) and advanced (multiserial) condition. In fact, the closest things to such intermediates that we have encountered are the incisors of *Prolapsus* and *Cyclomylus*.

We believe the presence of multiserial incisor enamel in all living hystricognaths cannot be taken as evidence of the descent of the Caviomorpha from the Thryonomyoidea, especially since the only known possible transitions from typical pauciserial to multiserial enamel are those found in the franimorph *Prolapsus* and in the primitive tsaganomyid *Cyclomylus*.

(19) *Ectoparasites* (by A.E.W.). Traub has recently (1980) reviewed the zoogeography of mammalian fleas (Order Siphonaptera), chewing lice (Order Mallophaga) and sucking lice (Order Anoplura), and its implications for the relationships and past geographic distributions of their hosts. Although his conclusions are stated as being supportive of an African origin for the Caviomorpha, a careful study of his text indicates that his data do not permit one to choose between transatlantic rafting of caviomorph ancestors and descent of both the Caviomorpha and the Old World hystricognaths from Eocene franimorphs with a Holarctic distribution.

The Anoplura infest sciurids, heteromyids, cricetids including gerbils and microtines, murids, dipodids, caviids, chinchillids, echimyids, bathyergids, *Pedetes* and *Thryonomys*, as well as lorises, lemurs and tupaiids. Traub considered (1980: 127–133) that these lice originated in North America, infested rodents as soon as the latter appeared, and spread through most groups of the order. He believed that the anopluran families probably date from the initial differentiation of the rodents. In fact, even the genus *Polyplax* may well be that old, since it "infests rodents (and occasionally other hosts as well) in most parts of the world, infesting such theraphions as phiomorphs like bathyergids and thryonomyids; caviomorphs like caviids, chinchillids and echimyids; dipodids; pedetids; the only true cricetids in the Ethiopian region; other cricetid rodents elsewhere; xerines and other sciurids; heteromyids; loricids; lemuroids; tupaioids; and leporids. The majority of these associations are surely primary" (Traub, 1980: 131). This suggests the possibility that *Polyplax* as a genus may date from the Eocene or Paleocene.

The distribution of the rodent Anoplura fits well with a North American (or Asiatic) origin of the order, and a worldwide distribution on and with the rodents. There are some peculiarities in their known distribution, probably due to a careful search not having been made of all possible hosts, but the data do not seem to me to give any support to an African origin of the Caviomorpha in preference to a North (or Middle) American origin.

One suborder of Mallophaga, the Amblycera, are primarily parasites of marsupials, with one family, the Boopidae, restricted to Australia and another, the Trimenopomidae, largely South American but extending into Central America (Traub, 1980: 122–127). A third family, the Gyropidae, are also South American, and perhaps were derived from the Trimenopomidae. The trimenopomids infest members of the Caviidae, Chinchillidae and Echimyidae, as well as marsupials, and the gyropids are found on these caviomorph families and the Dasyproctidae (Traub, 1980: 122), but both families are apparently absent on the Erethizontidae, Octodontidae, Abrocomidae, Hydrochoeridae, Dinomyidae and Cuniculidae. Clay (1970: 94–96) suggested that when the ancestral caviomorphs reached South America they had no amblyceran parasites; that they acquired trimenopomids from South American marsupials; that these then evolved into a distinct family, Gyropidae, on the caviomorphs; and that this was followed by another caviomorph infestation by other trimenopomids from South American marsupials. Certainly the Amblycera have no bearing on the origin of the Caviomorpha other than to suggest that these rodents came to South America from somewhere else.

"While members of the family Trichodectidae (suborder Ischnocera [Order Mallophaga]) are legion on fissiped Carnivora, Perissodactyla, Artiodactyla and Hyracoidea, they are found on only two groups of rodents, viz. an isolated branch occurring on the caviomorph Erethizontidae (New World porcupines) and a second distinctive taxon on the geomyids . . ." (Traub, 1980: 122). Traub gives no indication as to whether these lice were found on North American or South American erethizontids. However, the family clearly is primarily non-rodent and would seem to have a fundamentally Holarctic distribution. The erethizontids presumably acquired the lice from carnivores, perissodactyls or artiodactyls either in South or in North America, and the geomyids would have done the same in North or Middle America. The trichodectids therefore would seem to have no bearing on the origin of the Caviomorpha, except that they ultimately had a northern origin.

The fleas are a more complicated matter, both as to their own classification and as to their import for the relationships of their hosts. Traub believed (1980: 157) that fleas were in existence on Pangea and were represented from their separation on both Gondwanaland and Laurasia. He believed that the major flea families originated on the various continents presumably early in the Cretaceous, and that the subfamilies of modern fleas probably originated in the Cretaceous (1980: 113). The presence of the modern genus *Palaeopsylla* in the Baltic Amber of Europe shows that flea genera are very long-lasting, and thus infestation by members of a single genus of fleas does not indicate that two populations of mammals may not have been separated also for a very long time. Furthermore, another modern genus, *Ctenophthalmus*, according to Traub (1980: 143) is apparently the immediate ancestor of *Palaeopsylla*, so that it must be even older. It does not seem surprising, in that case, that *Ctenophthalmus* has a geographic distribution that is not at once readily understandable.

The large flea family Heteropsyllidae was apparently of northern (Laurasian) origin (Traub, 1980: 157). Some of its derivative subfamilies and tribes are South American and one is also Australian. One subfamily, the Ctenophthalminae, includes four tribes, two Neotropical, one Nearctic and one Holarctic and Ethiopian. Traub has suggested that these are indications of the African origin of the Caviomorpha, but, if one accepts the antiquity of flea taxa mentioned above, these data seem as readily explicable by having the infestations of the Caviomorpha and the African hystricognaths date from their common Eocene franimorph ancestors, who reached South America and Africa by independent routes.

Therefore, although Traub's conclusions read as though it is necessary to assume a transatlantic migration of caviomorph ancestors to explain the present distribution of the ectoparasites, I do not believe that this necessarily follows from his data. Traub informs me (letter dated Feb. 27, 1981) that "We are not as far apart on African-South American connections as our earlier correspondence may have indicated."

(20) *Other features* (by A.E.W.). There have been certain other supposed evidences of direct caviomorph-thryonomyoid relationships that were not cited by Lavocat (1973), but which were specified by Lavocat (1971a) or Hoffstetter (1975: 521, 522). These include the presence of a sacculus urethralis, serology, and fetal membranes, subjects concerning which

we feel that we cannot speak with any authority. We do not discuss these here, since we feel that we have previously (Wood and Patterson, 1959: 391–392; 413—414 and 414, n. 34; Wood, 1974b: 47–49; 1975a: 76–77 and Fig. 1; 1977a: 135) said everything that can be said on these topics until further evidence is produced by specialists in the various fields.

Recently, Sarich and Cronin (1981) have discussed rodent molecular systematics, concentrating on cricetids and hystricognaths. They mention, as one problem in this connection (*op. cit.*: 407) the "poor fossil record" of rodents, which might have been true a half century ago, but certainly is not today. They feel (1981: 419) that cricetids, "given their total absence in the appropriate North American fossil record, are, then, almost certainly of African origin . . . we see no great problem in having several cross the Atlantic in the late Eocene and early Oligocene from Africa to . . . South America." This total absence of cricetids from the Oligocene and Miocene of North America will come as a surprise to most mammalian paleontologists, as will the suggestion that they originated in Africa, where they are unknown in the Oligocene and rare in the early Miocene. Sarich and Cronin (1981: Fig. 7) illustrate their ideas of how the cricetids moved from Africa to South America to North America.

In discussing the hystricognaths, Sarich and Cronin mention (1981: 410) the "total lack of hystricognaths . . . in North America (except, of course, for the recent migrant *Erethizon*," apparently disregarding the description of hystricognathy in *Prolapsus* (Wood, 1972; 1973) and *Guanajuatomys* (Black and Stephens, 1973). They develop a molecular phylogeny of the Hystricognatha, with two groups, one including *Hydrochoerus*, *Cavia*, *Erethizon*, *Dasyprocta* and *Chinchilla*, and the other *Hystrix*, *Bathyergus* and *Petromus* (these two closely related), *Hoplomys*, *Proechimys*, *Myocastor*, *Octodon* and (probably) *Capromys*, *Geocapromys* and *Plagiodontia*. These two groups, they believed, crossed from Africa to South America separately, probably (although this point is not specifically made by them) after the invasion of South America by the cricetids.

A final surprise to a rodent paleontologist is Sarich and Cronin's mention (1981: 419) of "ancient murids in Australia . . . ."

In view of all the misconceptions that these authors were laboring under as to the fossil record of rodents, and the impossibility that their ideas of cricetid relationships are correct, there seems to me to be no reason why their data on hystricognath relationships could not fit equally well with our thesis of the origin of the suborder in some part of Holarctica and their subsequent invasion of South America from Middle America and of Africa from southwestern Asia, as with their proposal of multiple transatlantic hystricognath migrations from Africa to South America.

(21) *Summary* (by A.E.W.). As we have tried to make clear in this section, there are obvious similarities and obvious differences between the Caviomorpha and the Old World Hystricognathi. There is, however, not a single feature that characterizes all members of these two groups and that is found nowhere else among the rodents.

In our opinion, the most basic features (hystricognathy and the anterior deepening of the pterygoid fossa) are resultants of the lengthening of *M. pterygoideus internus*. The former occurs, incipiently to fully developed, among franimorphs. The condition of the pterygoid fossa is unknown in these forms; we suspect that it had deepened variable amounts. The dorsal opening of the fossa, in geomyoids, *Spalax* and *Aplodontia*, is presumably the result of parallelism. We suspect that these two characters (or rather, the lengthening of *M. pterygoideus internus* which caused them) are the only valid diagnostic features of the Hystricognathi.

There are a number of respects in which the Bathyergoidea are quite different from most or all other hystricognaths. These include their protrogomorphy (except *Bathyergoides*, which was hystricomorphous in a manner *sui generis*); the rather distinctive ear ossicles and their much greater fusion than in any other rodents; the absence of gyrencephaly; and their very different nematodes.

Three features separate the Erethizontidae from all other modern hystricognaths—the structure of the middle ear, the presence of an internal carotid artery, and the serology. These last two are so distinctive that the students of these subjects felt that the Erethizontidae deserve a separate sub- or infraorder of their own.

A number of features are shared with the completely sciurognathous ctenodactylids—hystricomorphy, fusion of malleus and incus, multiserial incisor enamel, and perhaps a sacculus urethralis. The ctenodactylids, however (Wood, 1977a), clearly have an ancestry entirely independent of that of the hystricognaths.

In several features, some or all of the Caviomorpha are clearly more primitive than any known Old World hystricognath, supporting the derivation of the Old World forms from the New, but making the reverse derivation difficult to accept. These include the rather widespread occurrence of non-fusion of the ear ossicles among caviomorphs, the presence of an internal carotid artery in the erethizontids, the four-crested molars of the primitive caviomorphs, and the universal replacement of dm_4^4 in the Deseadan caviomorphs. *Platypittamys* has less well-developed hystricomorphy than any known thryonomyoid or hystricid.

The ascending process of the alisphenoid has been reduced in living hystricognaths, though to a lesser extent in the bathyergids than elsewhere; its condition is unknown among franimorphs. A similar reduction characterizes muroids.

The amount of gyrencephaly is greater among hystricognaths than elsewhere in the order. However, as pointed out above (p. 490), gyrencephaly is merely a secondary result of increase of brain size, and a greater proportion of hystricognaths than of sciurognaths have attained large size.

A number of the features cited by Lavocat and Hoffstetter do not seem to us to have any significance whatsoever. These include the jugal fossa, generally absent and highly variable when present; the heaviness of the malar and the sinuosity of its anterior suture, both extremely variable and not confined to hystricognaths; the lateral strip of the supraoccipital, randomly present throughout the Rodentia; the cleft between the bulla and the squamosal, varying in its development from large to absent; the development of the maxillary on the floor of the orbitotemporal fossa, which does not differ in any respect from the primitive rodent condition; and the exceedingly variable retention of an independent interparietal.

It seems to us to have been demonstrated that the known thryonomyoids were morphologically incapable of having given rise to the Caviomorpha, and that the evolutionary trends within the thryonomyoids were such that it would be difficult to envisage any near ancestor that could have had such capabilities.

Some authors (e.g., Sarich and Cronin, 1981) have adopted the point of view that any evidence indicating a closer relationship of Old World and New World hystricognaths to each other than to any sciurognaths is evidence in support of transatlantic rafting of caviomorph ancestors, ignoring the fact that such a closer relationship would be just as expectable under our hypothesis of the derivation of the Caviomorpha from Middle American Eocene franimorphs.

We feel that these results indicate that the Suborder Hystricognathi is a reasonable concept; that the Caviomorpha and Bathyergoidea originated from the Franimorpha independently of the Hystricidae and Thryonomyoidea; and that there has been extensive parallelism among the later hystricognath groups after their separation from their Holarctic franimorph Eocene ancestors.

The Classification of the Suborder Hystricognathi

THE SUPERFAMILIES OF THE CAVIOMORPHA

It is rather generally agreed that there are four major groups within the South American Caviomorpha. This was first clearly recognized by Simpson (1945: 94–99, 209–213), who proposed four superfamilies: Erethizontoidea (Erethizontidae), Octodontoidea (Octodontidae, Ctenomyidae, Abrocomidae, Echimyidae, Capromyidae), Chinchilloidea (Chinchillidae) and Cavioidea (Eocardiidae, Caviidae, Hydrochoeridae, Dasyproctidae, Dinomyidae and Heptaxodontidae). Apart from various shufflings (the *Acaremys* group to the Octodontidae, the *Eumegamys* group to the Dinomyidae) and changes in rank (elevation of the Cuniculinae to family, lowering of the Ctenomyidae and Capromyidae to subfamily), about which there is inevitably less agreement, his arrangement has stood in its essentials. In our study of the Patagonian Deseadan rodents (Wood and Patterson, 1959) we stressed that the erethizontids occupied an isolated position in relation to the rest, and supported the removal of the dasyproctids, dinomyids, cuniculids and heptaxodontids from the Cavioidea, transferring them to the Chinchilloidea.

In recent years several publications dealing wholly or in part with Recent hystricognaths have appeared: Gorgas (1967) on the stomach and intestinal canal; Bugge (1971, 1974a, 1974b) on cephalic arteries; Woods (1972, 1975) on jaw, hyoid and fore limb musculature; Woods and Howland (1977) on the skin musculature; and George and Weir (1974) on chromosomes. Despite the unavailability of numerous forms, some of them critical, to one or another of these authors, much new information pertinent to caviomorph higher taxonomy has been made available by their studies.

The distinctness of the erethizontids is fully confirmed, all the new evidence separating them clearly from the other caviomorphs. Bugge, as did Moody and Doninger (1956: 52–53) before him, believed that they merit a sub- or infraorder of their own, and has proposed the Suborder Erethizontomorpha for them (1974a: 56, 70, 71, 73). He did so primarily on the basis of their retention of an internal carotid artery, a primitive structure that has been lost in all other living hystricognaths. It is difficult for us to assess the significance of this. Of the Deseadan rodents, the basicranial region is known only in *Incamys*, and here there is what might be a carotid foramen (p. 411). Apparently this area is preserved in a skull of *Branisamys*, SAL 102, but is still buried in matrix (Lavocat, 1976: Pl. 2, Fig. 1). The skull of the Fayum thryonomyoids is unknown except for maxillary fragments. It is possible, therefore, that Oligocene hystricognaths possessed this artery (*Reithroparamys* has what is, topographically, a carotid canal—Wood, 1962a: 122), and that only the erethizontids have retained it to the present. To further complicate matters, as indicated above (p. 485), possession of a "carotid" foramen by a rodent does not prove possession of an internal carotid artery (Wahlert, 1974a: 373).

In view of all of these uncertainties—and we believe that we are in very close agreement with Lavocat (1976: 82–83) regarding them—we doubt if possession of an internal carotid by erethizontids can safely be adduced to prove their separation at a sub- or infraordinal level. For the present at least, we retain them as a superfamily of the Caviomorpha, stressing, as we have before, that they were in all probability a very early offshoot from the ancestral stock.

Lavocat (1976: 82) wrote: "En raison

des traveaux de J. Bugge . . . Wood (1975) admet actuellement que les Erethizontidae pourraient être assez distants des autres Caviomorphes." This was "admitted" much earlier (Wood and Patterson, 1959: 377, 391–392). What Wood did state (1975a: 77) was that, if Bugge was correct in his concept of Erethizontomorpha, two invasions of South America would be required, the implication being that visualizing multiple successful transatlantic raftings became exceedingly difficult, and that North America was hence the more likely source area.

The coherence of the Octodontoidea is not called in question by the new studies of Recent forms. Unfortunately, too few of the numerous echimyid genera were available to the various authors to provide evidence with which to test the arrangement of the echimyid subfamilies suggested above (Fig. 6). Woods (1972: 190) found *Proechimys* (Heteropsomyinae) and *Echimys* (Echimyinae) to be "myologically more different from each other than would be expected if these genera were in the same subfamily." To judge from Gorgas' descriptions and figures, *Cercomys* and *Proechimys* (Heteropsomyinae), *Kannabateomys* (Dactylomyinae) and *Echimys* (Echimyinae) do show certain differences each from the others in stomach structure, but a larger representation is obviously needed. As indicated above (p. 394), we have transferred *Chaetomys* from the Erethizontidae to be a subfamily of the Echimyidae because of its retention throughout life of dm_4^4, a characteristic of later echimyids and otherwise (now that we have made this transfer of *Chaetomys*) unknown among the Caviomorpha.

Our knowledge of fossil capromyines has been limited to Recent or sub-Recent material. The description of a number of new subgenera and species of capromyines from Cuba (Varona and Arredondo, 1979) brings the record of this group in the Pleistocene or Recent of Cuba to 8 genera or subgenera and 19 species, which suggests that the capromyines were of considerable importance in the Antillean fauna before the arrival of man, and strengthens the possibility that they had been there for a considerable time. Rodriguez *et al.* (1979) have discussed the Cuban capromyine (capromyid in their terminology) genus or subgenus *Mesocapromys* as a capromyine whose numerous primitive, echimyid-like features demonstrate the derivation of the capromyines from the echimyids. We accept their identification of the significance of this form as a primitive capromyine, and believe that this reinforces our opinion that the capromyines deserve only subfamilial status.

Following Patterson and Pascual (1972: Fig. 12) we place the Ctenomyidae (as a subfamily) in the Octodontidae.

The "classical" cavioid families, Caviidae and Hydrochoeridae, differ sharply from other hystricognaths in being superficially non-hystricognathous, the angle leaving the ramus close to the plane of the incisor. The masseteric crest is high on the jaw and heavily built, with a deep groove extending back to the vicinity of the condyle between the crest and the side of the ramus; the crest does not reach the angle, the insertions of parts of the masseter in that region being marked only by faint ridges. The lower incisor is short, ending under M_2. On the basis of these distinctive features some authors (e.g., Miller and Gidley, 1918; Ellerman, 1940) have separated the hystricognaths into two grand divisions, one for these two families and another for all the rest. This, of course, was going too far; cavies and capybaras are specialized in these respects. The extinct and broadly ancestral family Eocardiidae (Scott, 1905: 465) possessed a more normal hystricognath angle and a slighter masseteric crest that is lower on the side of the jaw and runs back and down to the angle. The shortened incisor, however, had been acquired by Deseadan time (Wood and Patterson, 1959: 371). Hartenberger (1975) suggested that the Hydrochoeridae deserve to be ranked as a superfamily, largely on the basis of "*Villarroelomys*," which turned out not to be a hydrochoerid (p. 444). Capybaras clearly are good cavioids.

The principal uncertainties in caviomorph classification arise over the affinities of the Dasyproctidae, Dinomyidae and Cuniculidae. Are they cavioids, as Simpson and others maintained, or should they be placed elsewhere? The evidence advanced to support removal of dasyproctids, dinomyids and cuniculids from the Cavioidea was dental (Wood and Patterson, 1959: 324–329). All members of these families possess lower incisors of the usual length, and all of them have cheek teeth that differ in structure from those of cavioids *s.s.* Noting resemblances between the Deseadan chinchillid *Scotamys* and the contemporary dasyproctid *Cephalomys* in the structure of unworn or little worn molar crowns (the resemblances are real, no matter what interpretation one may wish to put upon them) and in general agreement with Schaub (*in* Stehlin and Schaub, 1951: 369–370), we transferred the families in question to the Chinchilloidea.

This proposal has of late met with less than universal approbation. Nearly all the new evidence is flatly against it. Gorgas (1967: 366–367) has found a close resemblance between the Cavioidea *s.s.* and the Dasyproctidae, etc., and decided differences between both and the Chinchillidae in stomach structure. Bugge (1971: 534) came to the same conclusion on the basis of the cephalic arterial system, as did Woods (1972: 190) for the muscular system and Vucetich (1975: 490) for the middle ear.

The evidence from chromosomes is interesting—and a little more complicated. George and Weir (1974: 90–93) distinguished four major groups of caviomorphs. One of them includes the Erethizontidae only, another the Octodontoidea. So far so good; it is in the composition of the other two that the surprise comes, especially in view of the virtually unanimous agreement reached—quite independently—by the other authors just mentioned. One of George and Weir's groups includes the Caviidae and Dasyproctidae, and the other the Cuniculidae, Hydrochoeridae and Chinchillidae (*Dinomys* was not available to them). They did, however, indicate (*op. cit.*: 100–101) a possible means of attaining (their Fig. 8) the *Hydrochoerus* and *Cuniculus* karyotypes "if it is assumed" that these forms "are cavioids with affinities with the Caviidae and Dasyproctidae respectively." We lay no claim to competence in karyology, but this possibility seems reasonable to us considering the weight of the other evidence.

Subjected to so heavy a barrage, we feel compelled to retreat and to replace the Dasyproctidae, Dinomyidae and Cuniculidae in the Cavioidea, although we admit to doing this without enthusiasm. Members of the group thus reunited agree in the total lack of a lateral process of the supraoccipital, in contrast to other caviomorphs, and most of them have a descending flange of the lacrimal, the dinomyids and *Cuniculus* lacking it. We wish to stress, however, that, within the Cavioidea as thus re-expanded, there is a split between the Dasyproctidae, Dinomyidae and Cuniculidae on the one hand and the Cavioidea *s.s.* on the other, and that this split occurred well prior to the Deseadan. We believe that this should be recognized in classification, and propose two subdivisions of the superfamily, that we call Series A and Series B (see below, p. 523). We offer no names for these subdivisions, since we consider the recent proposal by McKenna (1975a: esp. 40–42), according to which every identified stage in phyletic branching deserves special taxonomic status and a special name, to be a frightening example of the *inflatio ad absurdum* of higher categories that must inevitably result if cladistic classification is unthinkingly pushed to its logical limits. For a comment on a very similar proposal made nearly half a century ago, see Simpson, 1945: 25–26, footnote 4.

The position of the Antillean Heptaxodontidae, usually grouped with the Dasyproctidae, Dinomyidae and Cuniculidae, is very uncertain. *Elasmodontomys* (of which *Heptaxodon* is a synonym) is not an echimyid, as are most West Indian genera, since it replaces dm$_4^4$ (Wood and Patterson, 1959: 326), as does *Amblyrhiza*. It possesses a very large lateral process of the supraoccipital, a structure absent even in rudimentary form in the families under discussion and also in all cavioids *s.s.* The cheek teeth are hypsodont, but not hypselodont, whereas in the Deseadan chinchillid *Scotamys* the rootless condition had already been achieved. Having thus been maneuvered, so to speak, into a corner, we end by offering the very unsatisfactory suggestion that in our present state of ignorance the family may best be listed as Caviomorpha *incertae sedis* as to superfamily.

Previously (1959: 321–322) we were skeptical as to the distinctness of the Family Perimyidae of Landry (1957: 55, 59), which he placed in the Chinchilloidea between the Cephalomyidae and Chinchillidae. Vucetich (1975), however, has brought forward evidence from middle ear structure that has convinced us of its distinctness, as a family related to the Chinchillidae. Other reasons for the acceptance of this group as a valid chinchilloid family were presented by Bondesio *et al.* (1975: 441–442). As pointed out by these authors, the family name, however, should be Neoepiblemidae, dating from Kraglievich, 1926. These now join the Chinchillidae, relieving the loneliness of their otherwise solitary splendor within their superfamily. The resemblances between *Cephalomys* and *Scotamys* in the cheek teeth suggest the possibility of a common ancestry for the Cavioidea and Chinchilloidea early in caviomorph differentiation.

To conclude this section, we mention a well known fact. The Deseadan fauna is isolated in time. It is separated from the one following, the Colhuehuapian, by perhaps 10 m.y., and it itself followed upon a hiatus in the record that surely lasted as long or longer. The ancestral caviomorphs arrived in South America during this hiatus—just when within it is not known, although we suspect near its beginning—but it is very clear that the rodents encountered in the Deseadan are at a not inconsiderable remove from the beginning of the caviomorph radiation. The initial burst, however, had not yet spent itself by the Deseadan. As a result, we encounter forms that are difficult to classify with assurance. We have done our best to indicate in the pages above and in our previous contributions such doubts and reservations as we have on these scores. We are reasonably sure that the systematic positions of *Platypittamys*, *Migraveramus*, *Deseadomys*, *Incamys*, *Scotamys*, *Asteromys*, *Chubutomys*, and *Protosteiromys* are as we have stated. We have presented the evidence for placing *Sallamys*, *Xylechimys*, *Cephalomys*, *Litodontomys*, and *Branisamys*, but we realize that there is room for discussion concerning them, as by Lavocat (1976: 72–73). We agree with him that much is indeed "provisoire." Hoffstetter (1976: 8) has stated that "la classification des Caviomorphes, et surtout celle des formes anté-Miocènes, demande une révision d'ensemble." Presumably he was referring to classification at higher rather than lower taxonomic levels. Better material of the Deseadan forms will help here to some extent, but we suspect that even if we knew all of them from complete skeletons, problems might still remain. What is needed is the filling of the hiatuses so that lineages can be traced rather than inferred.

OTHER TAXONOMIC PROBLEMS OF THE HYSTRICOGNATHI

(1) *General* (by A.E.W.). One of the difficulties in trying to reach an accept-

able classification of the hystricognathous rodents is that, in our opinion, a number of authors shift between talking about hystricomorphs and hystricognaths as they go along, as though these two terms were synonymous. Recently, this approach seems to have been adopted by Lavocat (1978: 85). The hystricognathous rodents are those in which the angular process of the lower jaw arises from the lateral surface of the alveolus of the lower incisor. The hystricomorphous ones are those in which the origin of *M. masseter medialis* has spread forward through the infraorbital foramen to arise from the snout, resulting in great enlargement of the infraorbital foramen. These two features are *not* universally associated. There are sciurognathous hystricomorphs (Anomaluridae, Ctenodactylidae, Dipodoidea, Pedetidae and Theridomyoidea) as well as protrogomorphous hystricognaths (Bathyergidae, Tsaganomyidae, Cylindrodontidae, many reithroparamyids). *There is no possible way that the two of these features can be considered as both being always associated in a single rodent taxon and neither ever being present anywhere else.* As stated elsewhere (Wood, 1980c: 270), hystricognathy in rodents began to appear in the late Paleocene, and became gradually more fully developed. No trace of hystricomorphy is known before the middle Eocene (Theridomyoidea: Wood, 1974b: Fig. 4; Ctenodactylidae: Shevyreva, 1972b: 134–135, Fig. 1; 1976: Figs. 4–5, Pl. 1, Fig. 3b; *Prolapsus*: unpublished data).

As an illustration of this confusion of hystricognathy and hystricomorphy, we may quote Lavocat (1969: 1497) who stated that "Du point de vue systématique, nos conclusions confirment et complètent l'intuition fondamentale de Brandt en montrant que le sous-ordre des Hystricomorphes est une véritable unité naturelle, fondée sur des relations phylétiques précises et étroites." Aside from the fact that the "intuition fondamentale" should be credited to Waterhouse, 1839, rather than to Brandt, 1855 (who merely gave names to the groups that Waterhouse had identified), we believe that this statement by Lavocat is in complete contradiction of a vast amount of evidence. No return to the classification as proposed by Brandt is possible. One may assume that all the hystricomorphous forms are related, or that all the hystricognathous ones are, or that only those forms that are both hystricomorphous and hystricognathous belong together. But a combination of all three is impossible. It is a fundamental requisite that, in talking about these complicated matters, all authors should be careful to use precisely defined terms.

(2) *Infraorder Franimorpha* (by A.E.W.). Members of the Infraorder Franimorpha, varying from incipiently to fully hystricognathous, are known from the late Paleocene to early Oligocene (and possibly late Oligocene—Wood, 1980b: Table 1) of western United States and the late Eocene and earliest Oligocene of Mexico (Ferrusquía, 1978: 206). We believe them to have reached Asia at an unknown time or times during the Eocene (probably both early and late Eocene; see above, p. 449). Recent work (Wood, 1980b: 6; 1981: 86) has indicated that the North American Eocene-Oligocene Family Cylindrodontidae (represented in Central Asia, according to the classification we present here, by the Oligocene genera *Pseudocylindrodon* and *Morosomys* and by the Eocene to Oligocene *Ardynomys*) were at least subhystricognathous and hence were franimorphs.

The basic members of the infraorder are the rodents united by Wood (1962a: 117–118) as the subfamily Reithroparamyinae of the Family Paramyidae. As he pointed out (1962a: 117), the reithroparamyines were subhystricognathous; at least one genus (*Rapamys*; Wood, 1962a: 148) seems to have had an enlarged infraorbital foramen. Dawson (1977: 197, n.) has queried the justification of calling the Reithroparamyinae subhystricognathous, saying "The 'very incipient' hystricognathous condition of *Reithroparamys* (Wood, 1973, p. 30–31) seems to me to be still a sciurognathous jaw, 'incipient' only *a posteriori.*" This may be true, although the hystricognathy of *Reithroparamys huerfanensis* is quite well developed (Wood, 1962a: Fig. 46B), but as pointed out elsewhere (Wood, 1980c: 270) it is inconceivable that hystricognathy appeared instantaneously; it must have developed gradually, and the forms in which it was developing deserve to be called subhystricognathous or incipiently hystricognathous. Current taxonomic usage would seem to require them to be placed in the Suborder Hystricognathi.

The Franimorpha may be defined (modified from Wood, 1975b: 79) as: subhystricognathous to hystricognathous; protrogomorphous to hystricomorphous; with or without a distinct interparietal; alisphenoid does not extend much if any above level of glenoid cavity; at least sometimes a post-condyloid process on the mandible indicating the differentiation of the *M. masseter lateralis profundus, pars posterior,* deep division; molars cuspidate or crested, never a mesocone or mesoloph, sometimes a mesoconid but rarely a mesolophid; normal replacement of deciduous molars; and incisor enamel pauciserial or transitional from pauciserial to multiserial.

When Wood (1975b: 78–79) erected the Franimorpha, he placed the Reithroparamyinae in it, but left the other subfamilies of the Paramyidae in the sciurognath Infraorder Protrogomorpha, and left the Reithroparamyinae in the Paramyidae, which thus straddled the boundary between the two suborders. Wood still likes this idea—it indicates that the earliest known sciurognaths and hystricognaths were very closely related, but that they had already started to diverge in directions that would ultimately lead to such differences that their descendants were clearly very distinct from each other. Certainly no taxonomist living in Eocene time would have separated them at a level higher than that of subfamilies. Such a solution, of course, does not make for a neat set of cubbyholes. Patterson has now persuaded Wood that, although this is perhaps reasonable, it would not be generally acceptable.

We therefore recognize the Reithroparamyidae as a distinct family, that we define as follows: franimorphs with incipient hystricognathy; protrogomorphous in earlier and best known forms, infraorbital foramen enlarging in at least some later genera; bulla not co-ossified with the skull in earliest forms, but large and fused to the skull by middle Eocene; coronoid processes large and high; post-condylar process present at least sometimes; cheek teeth relatively simple, primitively tritubercular but with a distinct hypocone in upper molars and usually in P^4; metalophid incomplete, trigonid basin opening posteriorly; entoconid separated from posterolophid; transverse crest from entoconid toward hypoconid developing progressively, ultimately becoming a complete hypolophid; posterolophid progressively angulate at point of attachment to hypoconid; incisors narrow and compressed, enamel thin; skeleton, in the two cases where it is known, with elongate hind legs; size small to medium.

Guanajuatomys from the later Eocene of Mexico, and *Prolapsus* from the mid-Eocene of the Big Bend area of Texas, are both fully hystricognathous. *Prolapsus,* at least, had an enlarged infraorbital foramen. Both have been described, so far, on fragmentary materials. For both, better but undescribed materials are now available. The cheek teeth do not indicate close relationships between the two, or between either and any other well known group. We suspect that they belong to one or more Middle American franimorph families, but we know of no justification for the erection of such a family or families at the present time.

(3) *Cylindrodontidae and Tsagano-*

myidae (by A.E.W.). The Cylindrodontidae have long been recognized as a protrogomorph family, but the angular processes have been broken off from all described material. Recently a specimen was found that clearly had a hystricognathous angle and a small post-condyloid process (Wood, 1981: 86; in press a), which had led to the transfer of the family from the Protrogomorpha to the Franimorpha. The range of the family is middle Eocene (Bridger and Big Bend of Texas) through early Oligocene (Chadronian) and possibly late Oligocene of western United States, early Oligocene of Canada, earliest Oligocene of Mexico (Wood, 1980b: 6), as well as late Eocene and early (Ardyn Obo) and middle (Tatal Gol) Oligocene of central Asia. The incisor enamel was pauciserial in middle Eocene specimens of *Mysops* (Wahlert, 1968: 15), but uniserial in the early Oligocene *Cylindrodon* (*op. cit.*: 15).

Hussain *et al.* (1978: 101) suggested that the Chapattimyidae, from the middle Eocene of Pakistan, were ancestral, through *Petrokozlovia* of the middle to upper Eocene of central Asia (Shevyreva, 1976: 31) to the middle Eocene and later cylindrodonts of North America. This seems, on the face of it, most improbable. The tooth pattern of the Chapattimyidae does not suggest to me any affinities with later rodents other than the Ctenodactylidae. Structurally, the teeth of *Chapattimys* and *Saykanomys* from Pakistan (Hussain *et al.*, 1978: Pls. 1–6) are distinctly more advanced in their patterns than those of *Mysops* (Wood, 1973: Figs. 3, 4), as seems also to be true of *Petrokozlovia* (Shevyreva, 1976: Fig. 6). As indicated above (p. 504), the incisor enamel of the Chapattimyidae is pauciserial, which would allow them to occupy any position one wished.

For many years, Wood has argued (1937: 199; 1955: 171; 1970a: 17; 1974a: 50–53), in accord with the suggestion by Burke (1935: 3–4), that the cylindrodonts were ancestral, through the Asiatic *Ardynomys*, to the Mongolian genera *Tsaganomys*, *Cyclomylus* and their relatives. This view was accepted by Simpson (1945: 213), Wilson (1949: 93) and Schaub (1958: 1537). These genera were originally referred to the Bathyergidae (Matthew and Granger, 1923: 4; Teilhard de Chardin, 1926: 29–30), an assignment with which Landry (1957: 72–73) concurred. We here refer them to a distinct family, the Tsaganomyidae, related to both the Cylindrodontidae and the Bathyergidae.

There are many features in common between the cylindrodonts and the tsaganomyids, including both tooth and skull characteristics (Wood, 1974a: 51–52). The teeth of both are clearly four-crested in both upper and lower jaws, with no suggestions of any possible fifth crest or of a mesocone or mesoconid. The skull of the American species of *Ardynomys* (it is unknown in the Asiatic species) shows, among other features, a backward movement of the growing base of the upper incisor, so that it protrudes into the orbit in exactly the same area (although not not quite so far) and in the same manner as in the Tsaganomyidae. The arrangement in *Ardynomys* could probably also have given rise to the condition in the bathyergids, by an increase in the radius of curvature of the upper incisor, that would have pushed the growing base of the incisor upward and backward, so that it would have been enabled to grow backward. In the Tsaganomyidae, however, the upper incisor has extended its growing base back in the direction that had already been established in *Ardynomys*, as a result of which the large ridge, marking the course of the incisor across the anterior part of the orbit, forms a pronounced knob, lateral to M^{1-2}. There is much individual variation in the extent of this knob; sometimes there is an appreciable space below it above the alveolar border; in other specimens, the posteroventral end of the knob lies ventral to the occlusal surface of the upper cheek teeth. In these latter cases, the ridge impinged on the course of the infraorbital artery, vein and nerve to the infraorbital foramen; we are not sure, but presume that they passed lateral to the incisive ridge.

We are informed by Dr. J. H. Wahlert (*in lit.*, 15 March 1980) "that the enamel of both *Cyclomylus* and *Tsaganomys* is intermediate between pauciserial and multiserial. *Cyclomylus* is closer to pauciserial and *Tsaganomys* to multiserial." Later, he added (*in lit.*, 28 March 1980) "The incisor enamel of *Mysops* .... is pauciserial with a slight inclination and is very much like that of *Cyclomylus*. Relationship is allowed but certainly not demonstrated by this similarity."

We define the Tsaganomyidae as follows: protrogomorphous and hystricognathous rodents of large size; skull massive; occiput forwardly sloping, very wide; bulla flattened anteriorly; zygomatic arch extending posteriorly well beyond posterior root of zygoma; incisors procumbent, presenting nearly straight forward as in specialized bathyergids; upper incisors extending back into orbit, bases forming bulges on side of maxillae, sometimes ending lateral and ventral to occlusal surface of M^{1-2}; lower incisors extending back to beneath condyles; incisor enamel transitional from uniserial to multiserial; cheek teeth hypselodont, four-crested; deciduous teeth replaced in normal manner, dm^3 small, peg-like, dm_4^4 essentially molariform; numerous burrowing adaptations in skeleton and body musculature.

Genera. *Tsaganomys*, *Cyclomylus*, *Pseudotsaganomys* if not a synonym of *Cyclomylus* (Kowalski, 1974: 159), *Sepulkomys* and *Beatomus* if valid.

Distribution. Middle to late Oligocene, Central Asia.

(4) *Bathyergidae.* In the Bathyergidae, the elongation of the upper incisors has carried the growing base nearly straight backward. The incisors of *Bathyergoides* (Lavocat, 1973: Pl. 7, Fig. 5) and *Proheliophobius* (Lavocat, 1973: Pl. 5, Fig. 6) make ridges part way across the orbit, directed about as in *Ardynomys* and *Bathyergus*. In the other bathyergid genera (*Cryptomys*, *Georychus* and *Heliophobius*) the growing base lies posterior to M^3. We do not believe that it would be possible to evolve the structure of the advanced Bathyergidae from that of *Tsaganomys*, or vice versa, although both could be derived from that of *Ardynomys*.

One of us (A.E.W.) believes that the franimorph family Cylindrodontidae was directly ancestral to the Tsaganomyidae and, probably, also to the Bathyergidae, although the Oligocene cylindrodonts are clearly too specialized to be bathyergoid ancestors, in that they had acquired uniserial incisor enamel. However, "*Cyclomylus* has inclined pauciserial enamel that looks a lot like [that of] *Mysops* but is thicker" (Wahlert, *in lit.*, 13 February 1980).

At the time of Patterson's death, we had not completely agreed on how we wanted to treat the cylindrodonts and tsaganomyids. At least at one time, Patterson felt that a relationship such as that described above would require the transferral of the Cylindrodontidae from the Franimorpha to the Bathyergoidea. Wood objected, because the Bathyergoidea are fully hystricognathous and have a pterygoid fossa that opens into the orbitotemporal fossa, whereas the cylindrodonts are subhystricognathous with a closed pterygoid fossa. The classification given below (p. 572) follows Wood's opinion.

Stromer (1923: 263; 1926: 134) described *Bathyergoides neotertiarius* from the Miocene of Southwest Africa (Namibia) and indicated that it was a definite bathyergid. He implied, although he was not certain (1926: 148), that it was involved in the ancestry of the Bathyergidae. Lavocat (1973: 109), in his description of the East African Miocene rodents, gave the date of publication of *Bathyergoides neotertiarius* as Stromer, 1924, a paper that he did not include in his bibliography. Both Stromer (1926) and Romer *et al.* (1962: 1341) give the date of publication of the paper in question as 1923, a figure that we accept.

Lavocat (1973: 109–133) also adopted the view that *Bathyergoides* was ancestral, at least structurally, to the Bathyergidae. He (1973: 150–153) made a case for considering that *Bathyergoides* was an intermediate stage between the thryonomyoids and the bathyergids, but we believe that the evidence of probable relationships of the bathyergids to the Oligocene tsaganomyids and of the latter to the Cylindrodontidae, rules out that possibility. As noted above (p. 473), if nematode evidence is of any value in rodent taxonomy, it should be a strong support for the absence of relationship between the bathyergids and thryonomyoids. It is also significant in this connection that the bathyergids and tsaganomyids are all protrogomorphous, with no forward extension of *M. masseter medialis*, except in *Bathyergoides* and, perhaps, in *Cryptomys*. Tullberg (1899: Pl. 2, Fig. 17), cited by Lavocat (1973: 151) as conclusive support for the existence of hystricomorphy in bathyergids, shows the jaw muscles of *Cryptomys* (cited as *Georychus*) *coecutiens* with *M. masseter medialis* just visible in the lateral view of the infraorbital foramen. Comparison of Tullberg's lateral view of the cleaned skull (1899: Pl. 2, Fig. 14) with the figure of the jaw muscles (1899: Pl. 2, Fig. 17) suggests that the muscle was merely visible through the infraorbital foramen, and that there was no actual penetration—in other words, no origin of any of the fibers from the snout in front of the foramen. However, in his text, Tullberg states (1899: 79) that a difference of this form from *Georychus capensis* is ". . . dass Foramen infraorbitale . . . bedeutend weiter ist, als bei jener Art, und dass ein kleiner Teil des Masseter medialis . . . dieses Foramen hier in der That durchsetzt."

Lavocat's figure of the skull of *Bathyergoides* (1973: Pl. 7, Fig. 5) shows the fossa of origin of *M. masseter medialis* lying in front of, but largely above, the infraorbital foramen. The direction of the fibers of the muscle must have been nearly vertical throughout, rather different from the condition in the other hystricognaths. We interpret these conditions to mean that there has been significant selective pressure acting on the Bathyergidae to lengthen *M. masseter medialis*, but that true hystricomorphy has never been generally attained in this family.

Lavocat has demonstrated (1973: Pl. 23, Fig. 2; Pl. 26, Figs. 1, 6; Pl. 29, Figs. 1–9; Pl. 30, Figs. 1–6) that the cheek teeth of *Bathyergoides* (and probably of other bathyergids) are based on four transverse crests, with no trace of mesoloph or mesolophid (Fig. 30K), as is also true in the Tsaganomyidae. We have been unable to determine, either from Lavocat's description or from his pictures, whether there was normal replacement of the deciduous teeth or whether they were retained. It seems clear that the anterior tooth of the series generally had the same pattern as the subsequent teeth (Lavocat, 1973: Pl. 26, Fig. 1; Pl. 29, Figs. 1, 7; Pl. 30, Figs. 1, 2, 5), which suggests that they were P_4^4 rather than dm_4^4. There clearly was rapid wear of the cheek teeth, so that one tooth was considerably worn before the one behind it came into use. This, of course, is normal among burrowing rodents.

Lavocat has suggested (1973: 109, 122, 123) that there were four upper and five lower cheek teeth in *Bathyergoides*. This latter number was based on the jaw of no. SO 736, which has three cheek teeth in use, a fourth that had not as yet erupted, and what Lavocat identified as an alveolus at the front of the series (1973: Pl. 30, Fig. 4). We are somewhat hesitant in accepting four upper and five lower cheek teeth as being the correct formula for *Bathyergoides*, as it would be unique among rodents.

The whole matter of what teeth are present in bathyergids is still unsettled, but it is extraordinarily unlikely that P_3 is one of them (Lavocat, 1973: 123), since this tooth is otherwise unknown among the Rodentia. It seems probable that the increase of the cheek-tooth formula of bathyergids (up to $_6{}^6$) involves either the retention of $dm_4{}^4$ along with $P_4{}^4$, or the duplication of one or more teeth as in *Otocyon* (Wood and Wood, 1933: 43), or both. Certainly, if *Bathyergoides* possesses P_3, it could not have been descended from any known or reasonably anticipated Eocene or Oligocene rodent.

It seems improbable to us that the Bathyergidae secondarily became protrogomorphous, as Lavocat (1973: 151) proposed. We know of no cases where such a secondary development has been demonstrated. If, as seems clear, the forward growth of the origins of the branches of the masseter was an adaptation that increased the functional strength of the muscles that moved the incisors, it would be most amazing to find a secondary reduction of the jaw muscles in animals that had highly modified the incisors to permit their extensive use in burrowing. Such a reduction would have been much more remarkable than the retention of the primitive protrogomorphous condition by rodents that might have been helped had they evolved modified jaw muscles. The retention of protrogomorphy would simply mean that (as in the case of *Aplodontia*) the pertinent mutations had not occurred under the proper conditions. Reversion to protrogomorphy would require not only the reverse mutations, but also selection for less efficient jaw muscles.

All the features discussed above seem to us to demonstrate that the Bathyergidae could not have been descended from the Thryonomyoidea as Lavocat believed, and as Wood was once willing to accept (1975b: 942). We agree with the conclusions of Hill *et al.* (1957: 511) that the available data "point . . . emphatically towards a complete severance of the bathyergids from all" other living rodents.

Bathyergoides apparently was a primitive member of the Oligocene stock from which the Bathyergidae were derived, but was on a side line as shown by the fact that it had begun to develop hystricomorphy. Although we are not certain of the precise relationships of *Bathyergoides,* we see no valid reason for separating it from the Bathyergidae. The definition of the Family Bathyergoididae, as given by Lavocat (1973: 109)—"Famille de Bathyergoidea dans laquelle la structure des dents jugales est bien conservée."—is perhaps a valid generic diagnosis, but hardly seems worthy of familial separation.

We therefore define the Bathyergidae as follows: protrogomorphous to occasionally slightly hystricomorphous hystricognaths; skull and skeleton highly modified for burrowing; occiput broad, inclined forward; incisors hypertrophied and procumbent, with growing bases extended unusually far to the rear; cheek-tooth formula variable, with additional teeth of unknown nature; cheek teeth hypsodont to hypselodont, with crown patterns based on four transverse crests in both upper and lower teeth, with no trace of mesoloph or mesolophid; incisor enamel multiserial.

As we have tried to indicate, there are many similarities between the Tsaganomyidae and the Bathyergidae, as well as differences. It seems probable, however, that the two are related, both being descended from late Eocene or early Oligocene Asian cylindrodonts (but *not* from chapattimyids). We therefore unite the two families in a Superfamily Bathyergoidea. We have no feelings as to whether one or two lines crossed the boundary from the cylindrodonts to the Bathyergoidea.

(5) *Hystricidae.* Lavocat (1973: 160) included the Hystricidae, together with the Bathyergoidea and the Thryonomyoidea,

in his Infraorder Phiomorpha, and believed the common ancestry of all to have been primitive thryonomyoids. He stated (1969: 1496) that some East African forms "correspondaient parfaitement à ce que l'on pouvait attendre" of hystricid ancestors, but neither at this time nor later (1973: 153–158) was he more specific nor did he demonstrate how the hystricids could possibly be descended from anything that had begun to acquire the features that characterize the Thryonomyoidea. Lavocat noted (1978: 74), for the first time so far as we are aware, that, in the Hystricidae, there is "replacement of dP^4 by P^4," without apparently realizing that this makes all known thryonomyoids too advanced to be hystricid ancestors. Incidentally, it should be emphasized that, in the hystricids (in contrast to all known thryonomyoids) there is also universal replacement of dm_4 (dP_4) by P_4 at the ontogenetic stage normal for mammals.

As pointed out elsewhere (Wood and Patterson, 1970: 632–633; Wood, 1974b: 38) derivation of hystricids from Oligocene or later thryonomyoids is impossible, because all hystricids have a normal mammalian replacement of the deciduous teeth. The reverse direction, derivation of thryonomyoids from Eocene hystricids, would be possible, although we know of no evidence in support of such a derivation. Since no hystricids are known before the late Miocene, one can use one's imagination rather freely in determining the characteristics of Eocene hystricids. Lavocat (1978: 79) stated that "There does not exist in the lower Miocene of Africa any known form which could be said with certainty to be ancestral to the Hystricidae . . . ." In fact, one can go farther, and state with complete confidence that all known Oligocene and early Miocene African rodents can be completely ruled out as possible ancestors of the Hystricidae.

Where the hystricids lived in the mid-Tertiary and from what they were derived are pure guesses. Our guess would be that they lived in southern Asia, and that they were derived from the same hypothetical franimorph population that we believe to have been ancestral to the thryonomyoids. It is clear to us that there are no known rodents that could be considered to have been immediately ancestral to the Hystricidae.

If Lavocat was correct that the Hystricidae and the Thryonomyoidea should be united at the infraordinal level, the term "Hystricomorpha" ought to be used for the combination, since it has both long priority and very general acceptance. Lavocat's concept, "Phiomorpha," is essentially identical to the concept "Hystricomorpha" of those authors who are willing to accept the Caviomorpha as a distinct entity. The general acceptance of the term "Hystricomorpha," even when it is used in no more modern a sense than that of Brandt (1855) was shown by its usage, by all who were not taxonomists, at the symposium on the Hystricomorpha, held in London in 1973 (Rowlands and Weir, 1974).

We here consider the Infraorder Hystricomorpha to include, for the time being, only the Family Hystricidae. We believe that future discoveries will not demonstrate that the Bathyergoidea belong here. We have no opinion as to whether it will be shown that the hystricids and the thryonomyoids had a common ancestor that had evolved beyond the franimorph stage. If they did, they should be united in the Hystricomorpha; if not, the term Phiomorpha may be retained for the Thryonomyoidea.

(6) *Thryonomyoidea.* As indicated, we here restrict the Infraorder Phiomorpha to the Thryonomyoidea. Throughout this paper, we have used the latter term to avoid confusion, since our usage of "Phiomorpha" is so different from that of Lavocat. It is perhaps not necessary to retain three infraorders (Bathyergomorpha, Hystricomorpha and Phiomorpha) for the Old World Hystricognathi, but

this at least would emphasize our current complete ignorance of the interrelationships of these groups. It may even have been the case that the Eocene franimorph ancestors of the caviomorphs and thryonomyoids were more closely allied to each other than either was to the ancestors of the Hystricidae and Bathyergoidea.

It is perhaps presumptuous on our part to differ with Lavocat on the classification of the Thryonomyoidea, but there are a number of points on which we have come to differ with his conclusions, and we believe that we should present these and explain our reasoning.

We do not believe that *Thryonomys* and *Petromus* should be united in a single family, since we believe (as apparently Lavocat did likewise) that they belong to lines that were already separate in the lowest levels of the Jebel el Qatrani Formation. Wood (1968: 68–73) compared *Gaudeamus* with *Thryonomys*, and pointed out many similarities in tooth and jaw structure (cf. Wood, 1968: Figs. 14–15 and Wood, 1962b: 317–320, Fig. 2A–C); Wood's phylogenetic chart (1968: Fig. 17) showed *Gaudeamus* as approximately ancestral to *Thryonomys*. Lavocat (1973: 162) considered *Gaudeamus* as much too specialized to occupy such a position, although he kept the two together in the Thryonomyinae. We see no evidence of such precocious specialization, and believe that *Gaudeamus* was very close to, if not actually, the ancestor of *Thryonomys*. We believe that these genera belong to a group that early acquired highly crested cheek teeth, with the crests reduced essentially to three in all teeth except dm_4 (Wood, 1962b: Fig. 2A–B).

We do not believe that *Neosciuromys africanus* Stromer is a synonym of *Paraphiomys pigotti*, since *Neosciuromys* clearly had higher crowned teeth than *Paraphiomys* and had reduced the pattern of the lower cheek teeth to three transverse crests with no trace of subsidiary elements (Fig. 30G), whereas in *Paraphiomys pigotti* and *P. stromeri* (Lavocat, 1973: Pl. 26, Figs. 7–10; Pl. 27, Figs. 3–4, 9–10; Pl. 28, Figs. 6–7) the teeth are very brachyodont and there are always elements of the metalophulid II present.

In his table of tooth measurements (1973: 272, Table 14), Lavocat gives no measurements of lower teeth of *Paraphiomys pigotti* except one of 15.0 for what we believe is the length of the tooth row. He gives lengths of individual teeth of three specimens of *Paraphiomys stromeri* (including the type); these suggest that, in the latter species, the teeth are about 2 mm long. The lengths of the lower cheek teeth in Stromer's three specimens of *Neosciuromys africanus* range from 3.40 to 4.48 mm, so that they would seem to be appreciably larger than those of *Paraphiomys pigotti*. Finally, in *Neosciuromys*, M_2 is significantly larger than any of the other cheek teeth (Fig. 30G). *Neosciuromys* clearly was a member of the Thryonomyidae.

The specimen from the Jebel el Qatrani Formation of Egypt, described by Wood (1968: 48–51, Fig. 5F) as *Paraphiomys simonsi*, agrees with *Neosciuromys africanus* in the simplification of its pattern (although it has not gone quite so far), in its appreciable height of crown, and in the large size of M_2 (and M_3). There seems no basis, now that illustrations of all the Miocene forms are available (which they were not when Wood's 1968 paper was written) for not including this species in *Neosciuromys* as *N. simonsi*, a species somewhat smaller and more primitive than the early Miocene *N. africanus*.

Lavocat (1973: 21) defined the subfamily Thryonomyinae (=our Thryonomyidae) simply as "Thryonomyidae dont la structure des dents jugales n'est pas trés simplifiée." On the contrary, we believe, these forms clearly have very simplified tooth patterns, at least in comparison to the other Oligocene and Miocene thryonomyoid genera.

Petromus (Wood, 1962b: Fig. 1C–F)

has a very different tooth pattern from that of the Thryonomyidae, it being based on four transverse crests rather than three. This type of pattern is found in a considerable number of the Oligocene and Miocene African genera. The oldest family name available for these is Petromuridae of Tullberg, 1899 (as Petromyidae). We divide these, in general following Lavocat's opinions of the relationships of the various forms, but not his formal taxonomy (1973: 160), into three subfamilies: the Phiomyinae to include *Phiomys*, *Paraphiomys*, *Kenyamys*, *Simonimys* and *Epiphiomys*; the Diamantomyinae (we can see no justification for considering these a separate family) for *Metaphiomys* (Fig. 30E), *Diamantomys* (Fig. 30J) and *Pomonomys* (Fig. 30H–I); and the Petromurinae for *Petromus*. Lavocat placed *Metaphiomys* in a separate subfamily from the Miocene genera that he recognized (1973: 52, 160) as its probable descendants; this seems unwarranted to us, and we agree with his statement in the descriptive part of his paper (1973: 71) that he felt he should adopt a vertical classification and consider *Metaphiomys* the direct ancestor of *Diamantomys* and *Pomonomys*.

Lavocat's Family Myophiomyidae unites all the highly cuspidate genera, but it may not be a natural group. *Phiocricetomys* differs widely from the others in the very large size of the cingulum and the length of the anterior tooth, in the roundness of the individual cusps, and in the reduction of the dentition in the only known specimen to three cheek teeth (Wood, 1968: Fig. 16). Wood (1968: 74–75) concluded that the teeth were more probably M_{1-3} than dm_4–M_2; however (p. 496), perhaps they are dm_4–M_2. The apparent reduction of M_3 in *Elmerimys* (Lavocat, 1973: 105; Pl. 28, Fig. 11) could be a clue pointing in the same direction, if Lavocat's two subfamilies (Phiocricetomyinae and Myophiomyinae) really belong together. It is clear from Lavocat's text (1973: 103, 108) that he intended to include *Phiomyoides* in the Myophiomyinae, but that it was inadvertently omitted from his table on page 160. We believe that *Andrewsimys* also belongs here, on the basis of Lavocat's definition of the family, rather than in the Phiomyinae where he placed it. For the present, but with great uncertainty, we accept the union of Lavocat's Subfamilies Phiocricetomyinae and Myophiomyinae in the Family Myophiomyidae.

Lavocat (1973: 163) reported the discovery, in the Eocene of Pakistan, of an undescribed genus, which he suspected "puisse avoir déjà présenté toutes les structures essentielles des Phiomorpha . . . ." This citation was quoted by Wood (1975a: 75–76, 78) as an occurrence of the Phiomorpha in the Eocene of Pakistan. Although we are not sure, we believe that this is probably a specimen of the material described by Hussain *et al.* (1978) as members of the Chapattimyidae, a group that we do not believe had anything to do with the ancestry either of the Thryonomyoidea or of the Hystricidae. As those authors noted (Hussain *et al.*, 1978: 75), the only rodents they refer to this family whose lower jaws are known were sciurognathous. These seem most unlikely ancestors for the thryonomyoids. Lavocat has informed Wood (*in lit.*, 25 Jan. 1979) that he no longer believed "que les Rongeurs de l'Eocéne du Pakistan soient apparentés aux Phiomorphes. . . . ces Rongeurs ont tous un *très fort* mètaconule, ce qui ne s'accorde pas du tout avec la structure de *Phiomys andrewsi*."

Recently, Shevyreva and Chkhikvadze (1978: 418) have suggested, in a brief abstract, that a form represented by a lower jaw ("Sp. 3") from the middle Eocene of Kazakhstan, might have something to do with the ancestry of the "Phiomorpha." We doubt whether any fossils yet reported have any bearing on the immediate ancestry of the thryonomyoids.

Lavocat (1973: 20) cited the Infraorder Phiomorpha as dating from Lavocat, 1967, but listed, in his Bibliography, two papers of that date, Lavocat 1967A and 1967B. In the former paper, which discussed the Miocene rodents of East Africa and their relationships, he neither used nor defined the term "Phiomorpha." The expression "Superfamille des Phiomyoïdés" was used on page 60, and the term "Phiomyoidae" [*sic*] in the abstract (1967a: 57). The second paper, discussing the ear region of the theridomyoids, used the terms "Phiomorphes" and "Phiomorphs" in the French and English abstracts, respectively (1967b: 491), and the text makes comparisons of the theridomyoid ear with that of "Phiomorphes," not otherwise identified, the term being used three times (1967b: 498).

The only attempts by Lavocat at a definition of the Infraorder that we have found were in his East African monograph (1973: 20), and in his chapter (1978: 71) on the Rodentia and Lagomorpha in "Evolution of African Mammals." In the first of these papers, his definition seems hardly adequate: "*Définition*: Rongeurs d'introduction ancienne en Afrique, de provenance actuellement inconnue, de distribution actuelle tropicale à tempéré chaud, dans l'Ancien Monde exclusivement. Structure infraorbitaire primitivement hystricomorphe, très modifiée et régressé dans la famille des Bathyergidae. 4 ou 5 dents jugales, ou plus chez certains Bathyergoidea." His later definition was more illuminating: "Infraorder Phiomorpha Lavocat 1962. DIAGNOSIS. Lower jaw always hystricognath. Infraorbital structure primarily hystricomorph, greatly modified and secondarily reduced in some Bathyergoidea. Molar teeth morphologically tetra- or pentalophodont; greatly simplified in the Bathyergidae. Generally four cheek teeth, rarely three, sometimes five" (1978: 71). Even this definition does not separate the "Phiomorpha" from the Caviomorpha.

Lavocat concluded his monumental work on the early Miocene rodents of East Africa with the remark that above all we now need rodent faunas from the Eocene of South America and Africa (1973: 258). We heartily agree, and add Middle America to the list, along with more extensive rodent faunas from the Eocene of both north and south Asia.

CLASSIFICATION OF THE SUBORDER HYSTRICOGNATHI

We now summarize, in tabular form, our current ideas as to the classification of the Suborder Hystricognathi.

Suborder Hystricognathi Tullberg 1899
  Infraorder Franimorpha Wood 1975a
      Family Reithroparamyidae (new rank; Wood, 1962a as a subfamily)
      Family Protoptychidae Wood 1937
      Family Cylindrodontidae Miller and Gidley 1918 (excluding the Subfamily Tsaganomyinae; otherwise as given by Wood, 1974a)
      Incertae sedis as to family—*Guanajuatomys* and *Prolapsus*
  Infraorder Bathyergomorpha Roberts 1951
    Superfamily Bathyergoidea Osborn 1910
      Family Bathyergidae Waterhouse 1841 (Bathyergidae of authors, plus *Bathyergoides, Proheliophobius* and *Paracryptomys*, if the last is not a *nomen vanum*)
      Family Tsaganomyidae Matthew and Granger 1923 (as a subfamily)
  Infraorder Hystricomorpha Brandt 1855 (as a suborder; Tullberg, 1899 as an Infraorder)
      Family Hystricidae Burnett 1830
  Infraorder Phiomorpha Lavocat (first formal use as an infraorder by Lavocat, 1973: 20; first undefined use of the term "Phiomorphes" by Lavocat, 1967b: 491, 498; Lavocat, 1978: 71 dates the infraorder from Lavocat, 1962, in which paper neither "Phiomorpha" nor "phiomorphes" is used)

Superfamily Thryonomyoidea Wood 1955
  Family Thryonomyidae Pocock 1922
    Genera: *Gaudeamus, Neosciuromys, Thryonomys*
  Family Petromuridae Tullberg 1899 (as Petromyidae)
    Subfamily Petromurinae Ellerman 1940
      Genus: *Petromus*
    Subfamily Phiomyinae Schlosser 1911 (including Family Kenyamyidae Lavocat 1973)
      Genera: *Phiomys, Paraphiomys, Kenyamys, Simonimys, Epiphiomys*
    Subfamily Diamantomyinae Schaub 1958 (as a family; including Subfamily Metaphiomyinae Lavocat 1973)
      Genera: *Metaphiomys, Diamantomys, Pomonomys*
  Family Myophiomyidae Lavocat 1973
    Subfamily Myophiomyinae Lavocat 1973
      Genera: *Myophiomys, Elmerimys, Andrewsimys, Phiomyoides*
    Subfamily Phiocricetomyinae Lavocat 1973
      Genus: *Phiocricetomys*
Infraorder Caviomorpha Wood and Patterson 1955 (in Wood, 1955, as a suborder)
  Superfamily Erethizontoidea Simpson 1945
    Family Erethizontidae Thomas 1897 (Erethizontidae of authors less *Chaetomys*)
  Superfamily Octodontoidea Simpson 1945
    Family Octodontidae Waterhouse 1839 (including as a subfamily, Ctenomyidae Tate 1935)
    Family Echimyidae Gray 1825 (as Echimyna)
      Subfamily Echimyinae Murray 1866
      Subfamily Adelphomyinae Patterson and Pascual 1968
      Subfamily Dactylomyinae Tate 1935
      Subfamily Chaetomyinae Thomas 1897
      Subfamily Heteropsomyinae Anthony 1917
      Subfamily Plagiodontinae Ellerman 1940 (as Plagiodontiinae)
      Subfamily Capromyinae Smith 1842 (as a family)
      Subfamily Myocastorinae Ameghino 1904 (as a family)
    Family Abrocomidae Miller and Gidley 1918
  Superfamily Cavioidea Kraglievich 1930b
    Series A, new
      Family Eocardiidae Ameghino 1891
      Family Caviidae Waterhouse 1839
      Family Hydrochoeridae Gill 1872
    Series B, new
      Family Dasyproctidae Smith 1842
      Family Dinomyidae Alston 1876
      Family Cuniculidae Miller and Gidley 1918
  Superfamily Chinchilloidea Kraglievich 1940
    Family Chinchillidae Bennett 1833
    Family Neoepiblemidae Kraglievich 1926
  Incertae sedis as to superfamily
    Family Heptaxodontidae Miller and Gidley 1918

CONCLUSIONS (by A.E.W.)

The skulls, lower jaws and dentitions of rodents from the Deseadan Oligocene of Bolivia are described. *Migraveramus* is referred to the Octodontidae, *Sallamys* to the Echimyidae, *Incamys* to the Dasyproctidae and *Branisamys* to the Dinomyidae. Two undescribed dasyproctid genera are briefly discussed, as well as material referred by Lavocat (1976: 59–62) to the Patagonian genus *Cephalomys*. It is concluded that the Bolivian genus *Luribayomys* and the Uruguayan genus *Palmiramys* are *nomina vana*.

The largest part of the paper is the discussion section. The two contemporary theories of the origin of the Caviomorpha, namely transatlantic transportation of African waif migrants or island hopping from Middle America directly or through the Antilles, are discussed. It is pointed out that, whichever hypothesis is accepted, there has been independent evolution of the Old and New World hystricognath rodents for at least the last 40 m.y.

During the Eocene, the Atlantic Ocean was narrower than at present. In the earliest Eocene, there was a high latitude North Atlantic connection between Europe and North America that enabled paramyid rodents from the latter to reach the former. Europe at this time was separated from Asia by a wide waterway (at least, there is no evidence that any mammals were able to cross this waterway in either direction). The waterway closed during the early Oligocene (the "grand coupure"), permitting the invasion of Europe by a wide variety of Asian mammals.

South Asia (Pakistan, India, southeastern Asia) had, quite certainly, attained its present relationship with northern Asia at least by the middle Eocene, from which time a very considerable fauna of terrestrial mammals, almost all of north Asiatic aspect, are known. The complete absence of any reported autochthonous terrestrial south Asiatic faunal elements, other than possible moeritheres, suggests rather strongly that these southern areas may have been part of the Asian continent for a considerable period of time.

The exact Eocene relationships between Asia and North America are not known. There almost certainly was a high-latitude land connection in the late Paleocene or early Eocene, that permitted the transfer of early Eocene rodents from one continent (we believe North America) to the other. There was also a connection later in the Eocene that permitted the Cylindrodontidae to reach Asia and the Lagomorpha to reach North America.

Africa had long been isolated from the rest of the world. The African Eocene mammalian fauna was largely different from that of any other part of the world, although species questionably referred to the Palaearctic genera *Apternodon* and *Brachyodus* are present (Simons, 1968: 15). By the end of the Eocene, as these two forms indicate, Africa had established sufficiently close relationships with Palaearctica (presumably through southwestern Asia) to have permitted a few invasions. These must have included the thryonomyoid rodents (still unknown from the Asian Eocene or Oligocene).

South America, like Africa, was an island continent during the Eocene. There had been a situation earlier that permitted some waif dispersal between North and South America, whether in one direction or both is uncertain. At some unknown time after the mid-Eocene Musters, caviomorph rodents reached South America. And, at some pre-Deseadan date probably later than the arrival of the rodents, primates reached South America.

Rodents that show the initial stages of the development of hystricognathy (the migration of the angular process a short distance laterad of the incisive alveolus) appear in the late Paleocene of western United States. These and their later but generally similar descendants are united in the Infraorder Franimorpha. Hystricognathy increases among North American rodents during the Eocene, being completely developed in the middle Eocene *Prolapsus* from Texas. Hystricomorphy also appears in a number of franimorph lines. Although hystricomorphy appears in middle Eocene theridomyoids of Europe and ctenodactylids of Asia, all evidence indicates that neither of these groups ever developed, or gave rise to forms that developed, hystricognathy.

The Eocene fauna of Middle America is very poorly known. But there were a number of hystricomorphous and hystricognathous lines of rodents evolving in this area. Among these are the rodents of the Family Cylindrodontidae, which were hystricognathous but protrogomorphous. We believe that Middle American members of this family were ideal candidates, both in their geographic location and their structural features, to have been the ancestors of the Caviomorpha.

The Eocene relationships of North and South America are poorly known. There would seem, however, to have been periods of orogeny, forming chains of volcanic islands more or less along the course of the present Isthmus of Panama, in the middle Eocene, and there was unquestionably a chain of islands connecting Middle America and South America along the course of the present Antilles. Either of these would have provided a much easier invasion route to South America than the South Atlantic would have.

The Deseadan rodent fauna was compared with that of present-day northeastern Brazil. The frequency make-up at the various localities is strikingly similar in the two cases, with (usually) one species per locality the predominant one, but with relative abundances varying widely from locality to locality, even between those in close proximity. Rodents are one of if not the most abundant order in all Deseadan localities that have produced extensive collections.

In contrast, the early Oligocene rodents of Africa are much less diverse, taxonomically, than are the South American ones. In nearly every collecting locality, they are both individually and by taxa much less abundant than was the case with the Deseadan rodents. The only exception (Yale Quarry G) was a small quarry, producing only small mammals; here there was an overwhelming preponderance of one species of rodent.

The African Oligocene rodents were contrasted with their contemporaries, the rodents of the Porvenir local fauna of the early Oligocene Chambers Tuff Formation of Trans-Pecos Texas. Here six families of rodents are present, one with 3 and two with 2 subfamilies each, 13 genera and 15 species, all represented by a total of 44 specimens. Obviously, the diversity of North American early Oligocene rodents was vastly greater than that of their African contemporaries (only two closely related families, 3 genera and 4 named species plus 2 possible additional ones, are represented among 59 specimens from the early Oligocene). This clearly disproves the hypothesis that rodents reached Africa in the Paleocene or early Eocene.

The early Miocene rodents of East Africa present a very different picture. Here the numbers and diversity of the rodents are very similar to those in the South American Deseadan. We feel that this very clearly indicates that, in the early Oligocene, rodents had been in South America about as long as, in the early Miocene, they had been in Africa. The East African rodents consist of two groups—the descendants of the Oligocene forms, and a group of very recent immigrants, presumably from southwestern Asia (Bathyergidae, Anomaluridae, Pedetidae, Cricetidae, Sciuridae). Although the latter group is represented by more taxa than are the thryonomyoids, they make up less than 10% of the individuals that have been collected, and were obviously just beginning to establish a foothold on the continent.

The Oligocene rodents of Africa are compared with the Recent murids of Australia. These last apparently reached that continent from the East Indies about 4.5

m.y.b.p., and have since diversified in a continent where they had no competitors. The morphologic diversification of the Australian Pseudomyinae seems somewhat greater than that of the African Oligocene thryonomyoids (separated into three families not because they are that different but because their Miocene descendants achieved greater diversity).

That is, rodents would seem to have reached Africa no more (and probably less) than 4.5 m.y. before the deposition of the lower fossil wood zone, but to have reached South America two or three times as much before the Deseadan. Allowing for the various uncertainties, this would indicate that rodents had reached Africa in the latest Eocene, but that they arrived in South America about the middle of the Eocene.

The evidence for a close relationship between the Caviomorpha and the Old World hystricognaths, based on parasitic nematodes, has been milked for all it is worth. There apparently has been as much parallelism among heligmosomid nematodes as Wood thinks there has been among rodents; the entire basis for heligmosomid support of relationship between thryonomyoids and caviomorphs is, apparently, based on the genus *Paraheligmonella*, present in certain echimyids. If we interpret her meaning correctly, Durette-Desset (1971: 50) was very uncertain as to the accuracy of her assignment of this genus to the otherwise exclusively Old World family Heligmosomidae.

The oxyurine nematode *Evaginuris* is primarily known from caviomorphs. Two species have been reported from *Hystrix*, but both records deserve to be questioned. In one case, the host was a zoo specimen that could have been infected from contact with an American porcupine. The other species might also have been in a zoo specimen, and, in addition, the author of the species seemed to question either the accuracy of the identification of the host or the association of the nematode with that host. In any case, *Evaginuris* is an exceedingly doubtful support for thryonomyoid-caviomorph relationships.

Similarities occur between the fleas and lice of Old World and New World hystricognaths (Traub, 1980). These, we believe, indicate that the caviomorphs and the Old World forms are more closely related to each other than either is to any other living rodent, but there seems to be just as much support from these pests for a North or Middle American origin of the caviomorphs as for an African one.

A detailed analysis was made of the morphologic features that have been cited by various authors, especially Lavocat (1973: 168) as indicative of close relationships between the Oligocene and later caviomorphs and the Old World hystricognaths, similarities supposedly so great as to require the rafting of thryonomyoids from Africa to South America. Hystricognathy is common to both groups, but is likewise present in the North American Eocene-Oligocene franimorphs. This feature developed to permit lengthening of *M. pterygoideus internus.* This lengthening also resulted in deepening and eventual perforation of the dorsal margin of the pterygoid fossa. Due to damage in all available specimens, it is not known whether or not such deepening and perforation had occurred in the Eocene franimorphs. Hystricognathy, certainly, could have been inherited by both thryonomyoids and caviomorphs from Holarctic franimorph ancestors.

Some features (structure of the middle ear, presence of an internal carotid artery, and serology) separate the Erethizontidae from all other post-Eocene hystricognaths. These features would seem to indicate that they are more primitive than any of the Thryonomyoidea, and would permit them to have given rise to the Old World forms (which we do not believe happened) but would seem to be a complete barrier to their being descendants of thryonomyoids.

The Bathyergoidea are similarly isolated from all other post-Eocene hystricognaths, because of their retention of protrogomorphy, their rather distinctive ear ossicles with much greater fusion than occurs in any other hystricognaths, their smooth brains and their distinctive nematodes.

A number of the features cited by Lavocat and Hoffstetter are not, as they implied, hystricognath characters, but are widely distributed among rodents in general.

We conclude that the evidence indicates that the Caviomorpha and Old World hystricognaths are related; that it is morphologically impossible for the Thryonomyoidea to have given rise to the Caviomorpha or to the Hystricidae, but that evolution in either of the reverse directions would have been possible; and that the most probable scenario is for both the Thryonomyoidea and the Caviomorpha to have been derived from middle Eocene northern hemisphere franimorphs, even though these are still unknown in the Old World.

A classification of the Suborder Hystricognathi is presented. Among the Caviomorpha, several changes are made from our 1959 classification. These involve: transferral of the Chaetomyinae and Capromyinae to the Echimyidae, and of the Ctenomyinae to the Octodontidae; transferral of the Dasyproctidae, Dinomyidae and Cuniculidae from the Chinchilloidea to the Cavioidea; division of the Cavioidea into two Series, one for these three families and the other for the Eocardiidae, Caviidae and Hydrochoeridae; transferral of the Heptaxodontidae out of all recognized superfamilies to become *incertae sedis*; and recognition of the Neoepiblemidae as a second family of chinchilloids.

Among the Franimorpha, the Reithroparamyidae are raised to family status, and the Cylindrodontidae are included because they have recently been discovered to have been hystricognathous. The northern Asiatic Tsaganomyidae are considered to have been descended from the cylindrodonts but to be bathyergoids rather than franimorphs. It is concluded that there are no relationships whatsoever between the rodents from Pakistan included in the Chapattimyidae by Hussain *et al.* (1978) and either the Thryonomyoidea or the Cylindrodontidae.

We doubt that the modern Bathyergidae are secondarily protrogomorphous, as Lavocat (1973: 151) has proposed, and consider that *Bathyergoides* was specialized, not primitive, in its possession of partial hystricomorphy. The totality of the evidence seems to us to show that the Bathyergoidea were of northern Asiatic origin, evolving from Oligocene cylindrodonts, and that they have no relationship (except descent from primitive franimorphs) with other hystricognaths.

There continues to be no information as to the ancestry of the Hystricidae. We have no opinion as to whether they were ancestral to the Thryonomyoidea or whether the two groups evolved independently from the Franimorpha. We feel certain that the hystricids are not descended from thryonomyoids.

If the Thryonomyoidea and Hystricidae are related at the infraordinal level, they should be united in an Infraorder Hystricomorpha rather than Phiomorpha, since the former term has long priority and essentially universal recognition.

We recognize three families of the Thryonomyoidea—the Thryonomyidae, Petromuridae and Myophiomyidae. In the first family we place *Thryonomys*, *Gaudeamus* and *Neosciuromys*, the last being quite distinct from *Paraphiomys* with which Lavocat (1973: 22) synonymized it. This genus also includes the Oligocene species *N. simonsi*, described by Wood (1968) as *Paraphiomys simonsi*. We divide the Petromuridae into three subfamilies: the Petromurinae for *Petromus*; the Phiomyinae for *Phiomys*, *Paraphiomys*, *Kenyamys*, *Simonimys* and *Epiphiomys*; and the Diamantomyinae for *Metaphiomys*, *Diamantomys* and *Pomonomys*. The Myophiomyidae include two subfamilies: the Myophiomyinae for *Myophiomys*, *Elmerimys*, *Andrewsimys*, and *Phiomyoides*; and the Phiocricetomyinae for *Phiocricetomys*. We feel no conviction that these last two subfamilies deserve to be united at the familial level.

We assume that Lavocat's citation (1973: 163) of an undescribed Eocene genus from Pakistan that might be a thryonomyoid was a reference to one of the forms described by Hussain *et al.* (1978), in which case it is a ctenodactyloid and has no bearing on the problem of hystricognath relationships.

APPENDIX 1: LIST OF REFERRED SPECIMENS OF *SALLAMYS PASCUALI*, *INCAMYS BOLIVIANUS* AND *BRANISAMYS LURIBAYENSIS*

Sallamys pascuali. Eleven specimens in the Princeton collection: PU nos. 20906, a fragment of the right maxilla with P^4–M^1; 20907, a portion of the right ramus with part of the incisor and P_4–M_2; 20908, a portion of the right ramus with part of the incisor, roots of P_4 and much worn M_{1-2}; 20909, a fragment of the right ramus with part of the incisor and dm_4–M_2; 20910, a fragment of the right ramus with M_1 and the roots of P_4; 20911, a fragment of the left ramus with M_2 much worn and roots of P_4–M_1; 20912, a portion of the left ramus with part of the incisor and M_{1-2}; 20913, a portion of the left ramus with a broken incisor and the roots of P_4–M_3; 20982, an upper left molar, probably LM^1; 21727, a portion of the right ramus with M_{2-3} and the roots of P_4–M_1; and 21950, part of the right ramus with M_{1-2}. PU nos. 20908 and 20911 could be parts of one individual.

Incamys bolivianus. One hundred forty specimens in the MNHN, Princeton and MACN collections, as follows: SAL 119, Ldm^3–M^1; SAL 120, (R or L?) P^4–M^2; SAL 121, (R or L?) P^4; SAL 122, (R or L?) P^4; SAL 123, (R or L?) P^4; SAL 124, Ldm_4–M_2; SAL 125, Rdm_4–M_2; SAL 126, RP_4–M_1; SAL 127, LP_4; SAL 128, (R or L?) dm_4–M_3; "33 mandibules plus ou moins complètes SAL 129 à SAL 161" (Lavocat, 1976: 50); SAL 162, partial skull, and SAL 162A and 162B, associated rami of the lower jaw, type of *I. pretiosus*. The Princeton material includes PU no. 21726, skull and incomplete mandible found in connection, skull somewhat distorted but nearly complete, damaged in the orbital region and lacking the tips of the premaxillaries and incisors, the arches and antorbital bars, and part of the right bulla, mandible incomplete posteriorly on both sides and lacking tips of incisors and symphysis, but including all deciduous and permanent molars; PU no. 21945, skull with articulated mandible, missing the tip of the snout and left zygomatic arch, the ventral part of the mandible and the angles, but otherwise nearly complete and uncrushed; PU no. 20944, the anterior part of a skull, damaged and lacking all the cheek teeth; and 91 other specimens—PU no. 20953, incomplete premaxilla with broken I^1; PU no. 21728, maxilla with LM^{1-3} and partially erupted LP^4; PU nos. 20929, 20938–9, 20947, 20950–2, 20954–68, 20979–80, 21949, 21956, 21958–9, 21970–1, 21982 and 21985, fragmentary maxillae and isolated upper cheek teeth; PU nos. 20916–28, 20930–7, 20940–3, 20945–6, 20948–9, 20969–78, 20981, 21729–31, 21735, 21941, 21946–7, 21952–4, 21957, 21981, 21983 and 21987, fragmentary lower jaws and isolated lower cheek teeth. Of these, PU nos. 20965 and 20979, R and L P^4, may represent one individual; PU nos. 20954 and 20960, R and L P^4–M^2, another; and PU nos. 20958 and 20963, R and L P^4, a third. As indicated above (p. 429), MACN no. A 52-113, an isolated upper cheek tooth, identified by Wood and Patterson (1959: 362–4) as "?dasyproctid gen. et sp. indet.," belongs here.

Branisamys luribayensis. Thirty-one specimens in the MNHN and Princeton collections, as follows: a partial mandible with RP_4–M_1 and LM_{1-3} (SAL 103) was referred here by Hoffstetter and Lavocat (1970). Lavocat (1976: 33) referred SAL 104, (R or L?) M^{1-2}; SAL 105, fragment of the ramus with RP_4–M_3; SAL 106, erupting P_4 and M_1 (R or L?); SAL 107, LM_1 and posterior part of Ldm_4; SAL 108–115, eight partial mandibles with teeth; and SAL 116, jaw fragment (R or L?) with roots of cheek teeth. Our material consists of PU no. 20914, incomplete anterior half of a skull with broken incisors and damaged LP^4–M^3; PU no. 21960, a partial snout with both incisors, showing the naso-frontal contact and damaged ventral and lateral areas back to near the rear of the diastema; PU nos. 21732 and 21733, right and left maxillary fragments with little worn P^4–M^1, almost certainly representing the same individual; PU no. 21943, maxillary fragment with worn and broken RP^4–M^3; PU no. 21955, maxillary fragment with Rdm^4–M^1 and the root of dm^3; PU no. 20915, small fragment of maxilla with LP^4; PU no. 21944, mandible with RM_{1-3}; PU no. 21951, fragmentary mandible with RP_4–M_2; PU no. 21980, fragment of right mandible with P_4; PU no. 21987, fragmentary mandible with Rdm_4–M_1; PU no. 21986, isolated LM_2; PU no. 21734, fragment of mandible with RM_3 and damaged incisor; and PU nos. 21978, 21979, 22172 and 22173, fragmentary mandibles with incisors and roots of the cheek teeth. GB 014, Ldm_4, the type of *Villarroelomys bolivianus*, belongs here.

APPENDIX 2 (BY B.P.): VALIDATION OF *ACARECHIMYS*

The name *Acarechimys* was quoted ex ms. by J. L. Kraglievich (1965: 258) and credited to Patterson. The formalities, which it becomes necessary to supply, are as follows.

Acarechimys Patterson (*in* J. L. Kraglievich, 1965)

Diagnosis. Cheek teeth somewhat higher crowned than in *Protacaremys.* Upper molars with transverse lophs; anterolophs and posterolophs of M^{1-2} closely approaching buccal extremities of proto- and metalophs, uniting early in wear; posteroloph of M^3 reduced. Dm^4 tending toward reduction and loss of metaloph. Lower molars with variable metalophid, interrupted or absent in M_{1-2}, absent or interrupted in M_3, metaflexid deeper than mesoflexid in M_3. Dm_4 with metalophid united to metaconid or, rarely, falling short if it; anterior fossettid usually divided by anteroposteriorly or obliquely aligned neolophid. Masseteric crest stronger and more projecting than in *Protacaremys.*

Distribution. Santacruzian Miocene, Patagonia.

Type Species. Acaremys minutus Ameghino 1887 (Synonym: *Stichomys gracilis* Ameghino 1891).

Referred Species. Acaremys minutissimus Ameghino 1887 (Synonyms: *Stichomys diminutus* Ameghino 1891, *Sciamys tenuissimus* Ameghino 1894 and, provisionally, *Stichomys constans* Ameghino 1887).

The generic name commemorates the long-standing confusion of early octodontids (as "Acaremyinae" or "Acaremyidae") and echimyids, which is reflected in the synonymy above.

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ADDENDUM (by A.E.W.)

Since this manuscript was sent to the printer, several papers pertinent to our discussion have been received.

Evidence of the distinct nature of the Tertiary Middle American rodent fauna (p. 457) is given by Slaughter (1981), who described a rather distinctive new genus of geomyoid from the Miocene of Texas and Panama. He suggested (1981: 114) "that the Coastal Plain, perhaps all the way to Florida, was a northern portion of the Central American tropical biotic province . . . ."

Presence of the Hesperomyinae in Chihuahua in the early Pliocene (Jacobs and Lindsay, 1981), well before their earliest known occurrence in South America, should put an end to suggestions that they had an African origin. This also adds to the documentation of the Middle American fauna.

Vucetich (1980: 99–105) redescribed *Simplimus indivisus* and agreed with Fields that it is a dinomyid (see above, p. 427). She differs somewhat from our caviomorph classification. She transferred (1980: 10) the Dasyproctidae to the Cavioidea, as do we, but left the Dinomyidae in the Chinchilloidea, and did not mention the Cuniculidae. We continue to believe (see above, p. 511) that the Dasyproctidae and Dinomyidae belong together, in whatever superfamily they are placed.

Parent (1980: 166–169) described the middle ear of erethizontids. He concluded (1980: 253) that they were quite distinct from the other caviomorphs and that they perhaps diverged from the Caviomorpha before their arrival in South America. He also noted (op. cit.: 255) that the erethizontid ear region is the most primitive among all the hystricognaths he studied (which did not include the Eocene franimorphs *Reithroparamys* and *Protoptychus*). I believe that this monograph demonstrates the correctness of our interpretation (see above, p. 482) that he has shown that it would be impossible to derive the Erethizontidae from any Old World hystricognath. His conclusions support those we present above (p. 509). As previously, we accept the thesis that the Hystricognathi are a natural group.

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